The Ecological effects of Grazing by the White Rhino (*Ceratotherium simum simum*) at a landscape scale.

by

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Abstract

In this thesis I generated hypotheses concerning the top down effect of grazing ungulates on grass communities and fire behavior from work done within grazing exclosures in Hluhluwe iMfolozi Park. White Rhino had a large influence in controlling grass biomass in Hluhluwe, a high rainfall mesic savanna. Other smaller species of grazers could not replicate the effect of White Rhino when their grazing was removed. In Umfolozi, a semi-arid savanna, other species of grazer could replace the effect of White Rhino grazing and exert a controlling influence on grass biomass. Hence the relative importance of different species of grazers changed along a rainfall gradient.

When examined at a larger spatial scale I found that the removal of White Rhino led to a detectable change in grass biomass and in the grazing behavior of other species in the area of the removal.

The effect that herbivores exerted on the grass layer also had consequences for the movement of fire through the landscape by reducing fuel loads. Burnt areas were larger and less patchy in areas from which White Rhino had been removed in comparison to control areas. This effect was larger in Hluhluwe but still significant in Umfolozi. I suggest that both fire and grazing are in competition for the same resource, grass, and that each results in conditions favorable to the recurrence of that event (fire or grazing). This allows the system to switch between mammal and fire dominated states. Rainfall shifts the balance of this competition and in mesic savannas White Rhino appear to be the only animal capable of competing successfully with fire.

This work has application for the management of ecosystems that are influenced by top down control and for the maintenance of heterogeneity in mesic savannas.

Acknowledgements

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Contents

Notes

After a recent name change in order to more accurately reflect the grammar of the Zulu language the entire reserve in which this study was conducted is now known as Hluhluwe iMfolozi Park. I will refer to it in the text as HiP for the sake of brevity. However when referring to the two ends of the park I will refer to the northern end as Hluhluwe and the southern end as Umfolozi.

There are of course two species of Rhinoceros in the reserve the Black or Hook lipped Rhinoceros (*Diceros bicornis*) and the White or Square lipped Rhinoceros (*Ceratotherium simum*). Because the focus of this research is the White Rhino and its role in the ecosystem it can be taken as read that references made in the text to 'Rhino' refer to the latter species unless specifically stated.

The work in this thesis is all my own, other than where noted. However chapter 3 uses data collected over a number of years by the Zululand Grass Project and this has been collected by a number of different people.

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1 Introduction

African savannas are home to a high diversity of native grazers particularly of medium to large ungulates. The mechanisms allowing these multi-species assemblages of grazers to co-exist has been the subject of much research (Farnsworth et al. 2002). The grass layer upon which they feed consists of different species of grasses with different functional traits, allowing the various species of grazers to specialize their feeding niche to exploit these differences. For example, buffalo specialize in feeding on large quantities of coarse grass of low nutritional value whilst impala feed more selectively on smaller amounts of higher quality forage. These differences in diet may have developed through a shared evolutionary history as a result of past competition between grazers resulting in feeding niche differentiation (Jarman and Sinclair 1979, Connel 1980). Grasses have evolved in concert with their sympatric grazers (Augustine and McNaughton 1998), often showing adaptations to deal with the defoliation caused by grazing. Some grasses have distasteful secondary compounds or silicate matter in their leaves to discourage grazing (Stebbins 1981). Others have evolved towards a tolerance of grazing through adaptations in growth form (Belsky 1986) to the extent that, without the presence of grazing, they would be excluded by other species of grass. Such grasses are to be found on grazing lawns.

Grazing lawns were first described in the 1960's from countries such as Uganda and Zambia (Vesey-Fitzgerald 1960, Olivier and Laurie 1974) and were the product of nocturnal grazing by hippo (*Hippopotamus amphibious)*. These hippo lawns occurred at a distance of up 2 km from rivers and were characterized by short frequently grazed patches of grass within a matrix of taller grasses. Their distribution in the landscape was limited by the distance a hippo could travel in a night before returning to the river during the day.

Grazing lawns only really came to prominence with the work of McNaughton in the Serengeti (McNaughton and Georgiadis 1986, Augustine and McNaughton 1998). He demonstrated increased compensatory plant growth as a response to defoliation through grazing (McNaughton 1979). Grass re-growth is more nutritious with elevated levels of Nitrogen and Phosphorus compared with ungrazed grasses (Thompson-Hobbs 1996). Repeated grazing serves to maintain these grasses in a palatable juvenile form

(McNaughton 1984) leading to elevated green plant biomass concentrations, which in turn result in increased foraging efficiency for the grazing animals (McNaughton 1984). Grazing by herds of ungulates can accelerate the rate of nutrient cycling on grazing lawns through the concentrated deposition of urine and dung (McNaughton et al. 1997). McNaughton also proposed that grazing lawns were a product of co-evolution between grazers and grasses stating that 'conventional definitions of overgrazing may be inapplicable to native plant-herbivore systems' (McNaughton 1984, 1985) where the 'conventional definition' was that used in rangeland science (i.e. agricultural grazing or cattle farming). The co-evolution of grazers and grazing resistant traits of grasses has been demonstrated by both MacFadden (2000) and Mack (1982). Within Africa areas where native plant-herbivore ecosystems remain intact are now largely confined to game reserves and other conservation areas.

Despite the attention focused on grazing lawns elsewhere in Africa mention of them within the Southern African literature is rare, no mention of them being made in a recent survey of grasslands (O'Connor and Bredenkamp 1997). For much of the last century the prevailing philosophy was that short grass areas were a result of overgrazing inevitably leading to soil erosion and therefore highly undesirable. This viewpoint originated from rangeland science, from which ideas of veld management (i.e. natural systems) were largely drawn at the time. These theories catered for the needs of a small number of exotic domesticates such as sheep and cattle. The ideal grass sward was held to be long unbroken stretches of tall grasses (e.g. *Themeda triandra*) as this was a high biomass grass community which was palatable to cattle. It was assumed that native grazing animals had similar dietary needs.

There is growing evidence that grazing lawns are a feature of our natural history and not just anthropogenic artifacts of overgrazing by exotic livestock. Lawns support distinct communities of insects, birds and trees that are likely to have evolved together over millennia (Bond et al. 2001, Currie 2003, Krook 2005). It is only within the last ten years that the importance of grazer tolerant grass communities in southern Africa has been realised and work upon their ecological function has progressed. This change in thinking has come about in concert with a shift from thinking of communities, and savannas in particular, as stable climax communities to regarding them as dynamic systems dominated by disturbances. Current goals of management in conservation areas has moved to place an emphasis on preservation of biodiversity and this is widely implemented by attempting to manage for increased heterogeneity of habitat types within conservation areas as environmental heterogeneity is assumed to be the source of

biodiversity (Pickett et al. 2003). Hence the emphasis of savanna ecology has shifted to understanding the processes maintaining this heterogeneity.

The presence of lawn grass communities in HiP was noted by Owen Smith during his extensive studies of White Rhino (Owen-Smith 1979) but little research work was done on them until the late 90's (Swemmer 1998). In HiP grazing lawns bear more of a resemblance to the 'hippo lawns' described in earlier papers (Olivier and Laurie 1974), rather than those described by McNaughton. Lawns in the Serengeti are large in size and maintained by the seasonal movement, linked to rainfall, of sizeable herds of Wildebeest and other grazers over a large area. Lawns in HiP are smaller in size, ranging from just a few meters in diameter up to several hectares, and occur within a matrix of taller grasses and bush. They are maintained by the action of more sedentary populations of grazing animals confined within a fenced reserve. However it is of interest to note that within the last century there are records of large seasonal herds of wildebeest occurring near the settlement of Big Bend in Swaziland only 200 km north of HiP (Gosnell 2001). Hence it is distinctly possible that such large scale movements of herbivores did occur in the area including HiP in the not too distant past and that these may have played a role in shaping the ecology of the area.

Grazing lawns in HiP are not only structurally but also floristically distinct from taller grass areas. Hence grass species within HiP can be separated into two groups. Species of grass commonly found on grazing lawns (hereafter lawn grasses) include *Urochloa mosambicensis, Dactyloctenium australe* and *Digitaria longiflora.* Under grazing pressure lateral buds on lawn grasses have the ability to grow horizontally as either stolons or underground rhizomes and these have the ability to send out new roots thereby forming new individuals and hence propagating vegetatively. As a result of this they are short in stature. Taxonomically they are members of the sub-tribe Chloridoidea.

In contrast bunch grasses are usually to be found within the sub-tribe Andropogonae. They include *Themeda triandra, Heteropogon contortus* and various species of *Hyparrehenia, Bothriochloa* and *Cymbopogon.* They do not posses the ability to grow by stolons and lateral buds grow vertically giving rise to tussocks. They are reduced as result of heavy grazing. However in the absence of grazing pressure they grow tall and as a result shade out lawn grasses which in turn become reduced in numbers by their inability to compete effectively for light (Belsky 1986). Hence lawn grasses require grazing pressure to persist in the environment. Their resistance to grazing and high productivity may be an example of the co-evolution suggested by McNaughton.

Another important distinction is that bunch grasslands burn readily due to their high standing biomass, whilst lawn grasses do not have sufficient fuel to carry a fire. The reduction of grass fuels caused by heavy grazing has long been thought to reduce fire intensity and fire frequency which, in turn, is thought to promote establishment and growth of woody species which would otherwise have been retarded by fire (Scholes and Archer 1997, Van Auken 2000, Langevelde et al. 2003). Hence 'overgrazing', causing expansion of short grass swards, has been widely suggested as a cause of would promote encroachment of woody species into savannas(Ward 2003).

White Rhino are grazing megaherbivores (defined as animals with an adult weight of over 1000kg (Owen-Smith 1988). Because of their size adult megaherbivores are seldom prey to non-human predators and their populations become solely limited by food resources. Owen Smith (1988) argued that megaherbivores are likely to be keystone herbivores because their populations are likely to be food, rather than predator-limited and because of their large food requirements per individual. Keystone species exert disproportionately large effects on an ecosystems function and composition, relative to their number (Power et al. 1996) and it has been suggested that White Rhino may play a greater role in the creation and maintenance of grazing lawns in HiP than other species of grazer (Owen-Smith 1979).

The megafauna alive today represents a small fraction of the large and diverse megafauna that inhabited the earth from Quaternary period to the Pleistocene epoch. At the end of the Pleistocene the majority of these disappeared (Martin and Wright 1967, MacFadden 1998) with 13 of 21 genera becoming extinct. What was once a global megafauna is now confined to Africa and tropical Asia. It has been argued that the extinction of the Pleistocene megafauna could account for large changes in ecosystem structure, e.g. from open grassy to more closed woody communities in the Holocene (Owen-Smith 1987, 1989) and that these habitat changes may have accounted for the concurrent extinction of other smaller bodied mammals. The implication is that, at least some of the megaherbivores had a major influence in the top down control of ecosystem structure. Top down effects of extant megaherbivores have been shown for browsers (Prins and van der Jeugd 1993, Bond and Loffel 2001, Fritz et al. 2002) and grazers (Verweij et al., Knapp et al. 1999) (though bison in the latter example are not strictly classed as megaherbivores).

In this thesis I want to address the following questions: Are grazing lawns a product of top down control of ecosystems as is suggested by work in the Serengeti and

elsewhere or is their distribution controlled by other abiotic (or bottom up) factors such as soil type and rainfall? If grazing lawns are biologically controlled by top down forces which ones are the most influential? If grazing lawns require grazing for their persistence is this an effect of all species grazers or are some species more influential than others. It has been suggested that as a megaherbivore, the White Rhino is particularly influential in maintaining grazing lawns(Vincent 1970, Owen-Smith 1979). The implication of this is that if White Rhino are removed from the system the distribution of grazing lawns will be reduced in extent along with any other species that depend these areas. If a reduction in grazing pressure does lead to a switch in grassland state what might the consequences be for the rest of the ecosystem? Flannery (2002) has suggested that the loss of a megafauna can result in larger and more frequent fires in a system due to increased fuel loads.

In this thesis I examine what role the White Rhino play in the maintenance of grazing lawns compared to other species of mammalian grazers and also whether lawns, and perhaps Rhino, can alter the behaviour of fire in a system. This work forms part of a larger project, the Zululand Grass Project (ZLGP) which examines the factors controlling shifts in habitat in a natural system. I have tried to focus particularly on landscape scale analyses in order to test theories developed during ZLGP at large scales. I test these theories in Hluhluwe iMfolozi Park (HiP) which has a unique and unbroken history of habitation by White Rhino and also has the highest densities of Rhino in the world. However the Rhino population is still regulated by natural processes giving us a rare opportunity to study grass/grazer interactions in an intact natural system with an extant grazing megafauna.

Thesis structure

This thesis is divided into the following chapters:

- Chapter 1: Chapter introducing the subject and other relevant themes to be tested in this thesis.
- Chapter 2: Description and relevant history of study site.
- Chapter 3: A study of the effects of White Rhino grazing using fenced exclosure plots and the generation of hypotheses to be tested later in the thesis.
- Chapter 4: Construction of a spatial database of White Rhino removals necessary to test the above hypotheses at a landscape scale.
- Chapter 5: A landscape scale experiment designed to test the effects of White Rhino grazing at a large spatial scale.
- Chapter 6: Presents the results of a study investigating whether White Rhino grazing can, through its effects on the grass layer affect fire regimes.
- Chapter 7: Concluding discussion of results in a wider scientific context.

2 Study site: Hluhluwe iMfolozi Game Reserve

Hluhluwe iMfolozi Park is situated in the north of the province of Kwa-Zulu Natal in the Republic of South Africa (Figure. 2.0). The park is situated in the heart of Zululand approximately 50km west of the Indian ocean at the point where the coastal plain first starts to merge with the escarpment that eventually rises up to the central highveld plateau of Africa. It covers an area of just over 90,000 hectares.

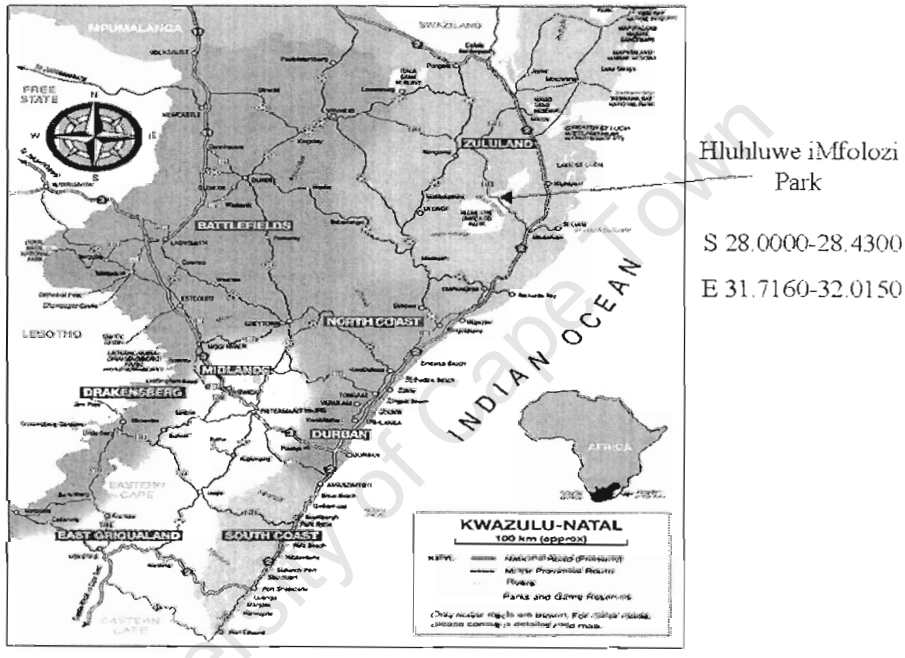


Figure. 2.0. Map showing the location of Hluhluwe iMfolozi Park in Kwa-Zulu Natal and Africa.

Geology

The geology of the area is diverse with 13 different geological formations representing all the major geologies of KZN. These include ancient granites (Nseleni Gneiss), Natal group sandstones, Ecca group mudstones and shales and basalts of the Sabi river formation. These different geologies are characterized by intense fracturing and faulting which occurred during the break up of the Gondwanaland super-continent (King 1970). Soils are likewise diverse with properties related to the underlying geology rather than landscape position – i.e. the area lacks the catenary sequences typical of old land surfaces. Most of the area has clay-rich structured soils derived from shales,

mudstones or dolerite outcrops. Many bottomland soils have a duplex character with dense, compacted subsoils. Sandstones support grey, sandy soils often with hydromorphic features (mottling) in the sub-soil. Altitudes within the park range from 20 to 580 meters above mean sea level. The topology of the reserve features steep sided hills and valleys to the north of the Hluhluwe river. The corridor region is characterized by gently rolling hillsides sloping down to the Black Umfolozi river. The Umfolozi section of the reserve is dominated by the two Umfolozi rivers which have wide floodplains associated with them separated by low rolling hills broken by occasional higher outcrops such as Nqabeneni and Mpila hills. The western edge of Umfolozi is bounded by a high ridge of hills running along the boundary of the reserve. Figure 2.1 gives a map of the reserve.

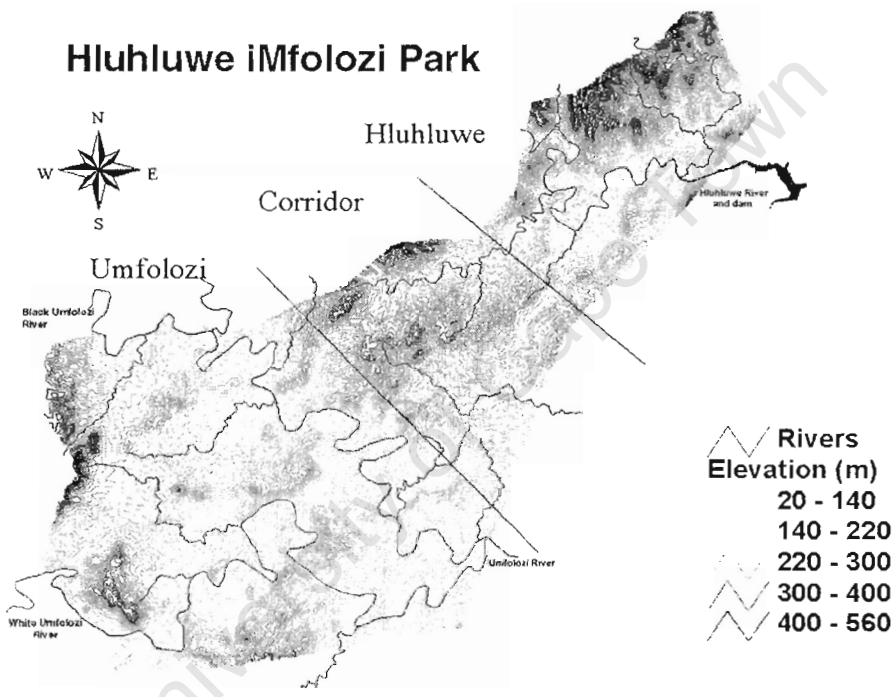


Figure 2.1 Map of Hluhluwe iMfolozi Park showing areas mentioned in the text, contours and major watercourses.

Climate

The climate is sub-tropical with hot wet summers and cooler dryer winters. Winter temperatures average 18°C (range 29.2-4.9°C) occasionally dropping below freezing point in the low lying river valleys during clear winter nights. In summer temperatures average 33°C (range 42-15°C : ZLGP data). Mean annual rainfall measured at Hilltop camp in Hluhluwe is 979mm with a range of 1594 to 670mm. However this figure is not representative of rainfall in the rest of Hluhluwe game reserve because of Hilltop camp's lofty position, (the amount of rain generally increases with altitude

(Balfour and Howison 2001). Rainfall at Memorial Gate averages 771 mm per year with a range of 442-1191mm and I regard these figures as more typical of Hluhluwe in general. Annual rainfall in Umfolozi is lower with a mean of 630mm and a range of 1127-333mm per year. (Rainfall data is based on (Pattenden 1988)) Classified on basis of rainfall this makes Umfolozi a semi arid savanna and Hluhluwe a mesic savanna. Rainfall alternates between wet and dry phases with a period of between 4 and 10 years (Balfour and Howison 2001). Most rain falls between the months of October and March. Annual variation in rainfall at both ends of the park is given in Figure 2.2 and the mean rainfall and temperatures for each month in Hluhluwe and Umfolozi are given in Figure. 2.3.

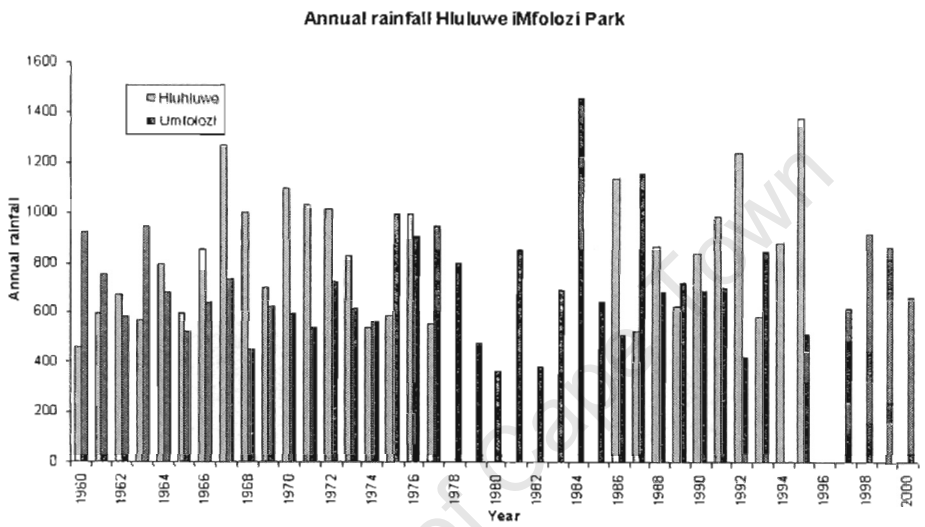


Figure 2.2. Long term variation of annual rainfall (mm) in Hluhluwe iMfolozi Park for Hluhluwe (Memorial gate) and Umfolozi (Mpila camp). Note that some years are missing although data is complete for all years shown.

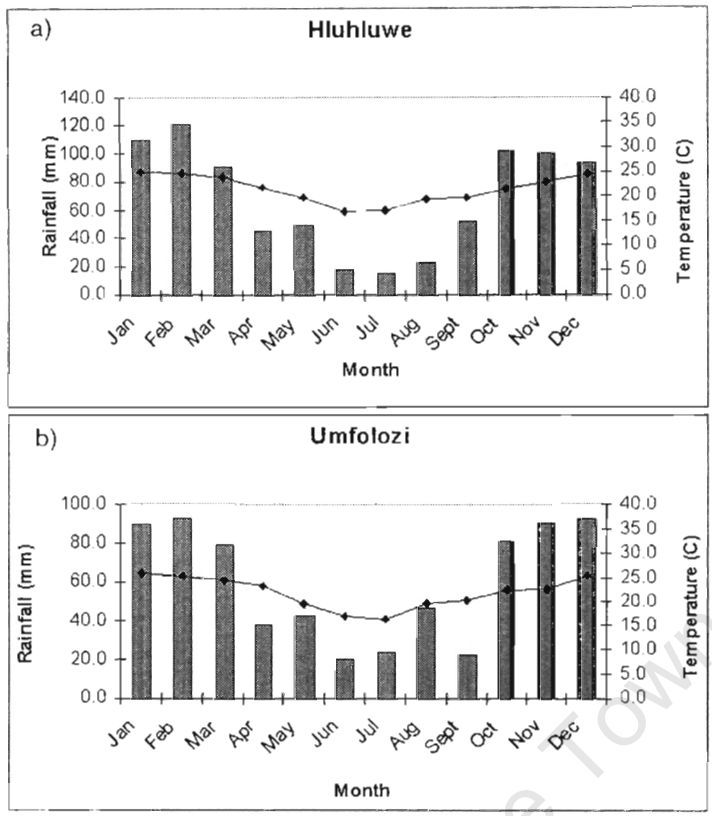


Figure 2.3. Mean monthly rainfall in mm (bars) and mean temperature °C (lines) for a) Hluhluwe and b) Umfolozi. Rainfall data for Hluhluwe is the monthly average rainfall for the period 1964-2001 measured at Memorial gate and for Umfolozi is the average monthly rainfall for the period 1959-2002 measured at Mpila camp (EKZN wildlife data). Monthly average temperatures are taken from ZLGP experimental sites.

Vegetation types

Because of its diverse topography and range of soil types the park supports a number of different habitat types. The hills and valleys of northern Hluhluwe are clothed with remnants of Coastal Scarp forest containing Wild Plum (*Harpephyllum caffrum*) and White Stinkwood (*Celtis africana*). Riverine valleys contain a fringing forest that includes species of fig (*Ficus spp.*), Weeping boer-bean (*Schotia brachypetala*) and stands of Tamboti (*Spirostachys africana*). The rest of the reserve is a complex mixture of open grasslands, savannas and thick bush. Savanna woody species include the shrub *Dichrostachys cenera* and various species of *Euclea* and *Acacia*. Grasslands range from tall fire prone communities dominated by *Themeda triandra* to short highly grazed lawn grass communities featuring such species as *Urochloa mossambicensis*, *Digitaria longiflora* and *Dactyloctenium australe*. Prominent trees in savanna areas include the Marula (*Sclerocarya birrea*) and *Acacia burkei*. There is some turnover in species between the two ends of the park with *A. karroo* and *A. nilotica* being common in

Hluhluwe but replaced by *A. tortilis* and *A. nigrescens* in Umfolozi. Whately and Porter (Whateley and Porter 1983)give a detailed classification of vegetation types. The park falls under the Zululand Thornveld (type 6) and Lowveld (type 10) classifications of Acocks (1953).

There has been a large amount of change in the amount of the various vegetation types (forest, bush and long and short grass communities) in the reserve over the last 70 years. Bush encroachment has been substantial despite efforts to control it, particularly in the high rainfall northern end of Hluhluwe (Wills and Whateley 1983). There also appears to have been a parallel increase in bunch grass communities at the expense of short grass communities over the same period (Bond et al. 2001). Despite some analyses of the bush encroachment problem the causes of this phenomenon remain unclear (Wills and Whateley 1983, King 1987, Watson 1995, Skowno et al. 1999). However the observed changes do indicate the presence of a dynamic ecosystem within the park. These changes have been compounded by the invasion of the alien shrub *Chromolaena odorata,* which can form dense stands especially in the northern end of Hluhluwe.

Fire Management

Fire management within the reserve only became a matter of policy in 1956 (Balfour and Howison 2001). Before that fires were either suppressed or burning was very haphazard. Since that time fire has been used in an attempt to control woody plant encroachment and in order to remove moribund grasses. The area of the park that burns is related to rainfall with a larger proportion of the park burning in wet years due to increased fuel loads. The majority of fires occur between June and October with August being the peak fire month. Mean fire return period is 3.8 (median 1.3) years. Data comes from (Balfour and Howison 2001) and covers the period 1956 to 1996.

Animals

The park supports a large number of grazers, the major (i.e. larger) ones are listed: Wildebeest (*Connochaetes taurinus*), Zebra (*Equus quagga*), iMpala (*Aepyceros melampus*) (which also browse seasonally see (Botha 2001), White Rhino (*Ceratotherium simum*) and Warthog (*Phacochoerus africanus*) all favor short grass areas when available. Buffalo (*Syncerus caffer*) prefer to feed on taller, coarser grass.
The major species of browsers are: Giraffe (*Giraffa camelopardalis*), Black Rhino (*Diceros bicornis*), Elephant (*Loxodonta africana*), Kudu (*Tragelaphus strepsiceros*) and iNyala (*Tragelaphus angasi*).

The park has a full compliment of carnivores including: Lion (*Panthera leo*), Leopard (*Panthera pardus*), Cheetah (*Actinonyx jubatus*), Wild Dog (*Lycaon pictus*) and Spotted Hyena (*Crocuta crocuta*). Jackal (*Canis mesomelas*) have however gone locally extinct.

Predator control was carried out until about 1950 with a particularly extensive campaign occurring between 1912-18. This took the form of destroying 'vermin' such as hyena and wild dog when encountered (Vaughan-Kirby 1916). Lion and cheetah were reintroduced in the 1960s and wild dog in the 1980s.

Populations of all of the major herbivores and carnivores have fluctuated widely as a result of both disease and human intervention some of which is detailed below. The results of the most recent herbivore census are given in table 2.0. Figure 2.4 illustrates the contribution to herbivore density of the various species.

Table 2.0. Results of the 2004 herbivore census (Rensburg 2004). Average weight of species is taken from Kingdon (1997).

Species	2004 census	Average weight (kg)	biomass (kg)	Density(kg/ha)
Buffalo	3,152	650	2,048,800	22.76
Kudu	1,239	220	272,580	3.03
Nyala	7,490	100	749,000	8.32
White Rhino	1,731	1,700	2,942,700	32.70
Giraffe	719	1,200	862,800	9.59
Wildebeest	3,082	260	801,320	8.90
Warthog	3,184	75	238,800	2.65
Zebra	3,389	250	847,250	9.41
Impala	24,471	60	1,468,260	16.31
Waterbuck	707	210	148,470	1.65
Black Rhino	301	1,200	361,200	4.01
Elephant	330	2,800	924,000	10.27
Total			11,665,180	129.61

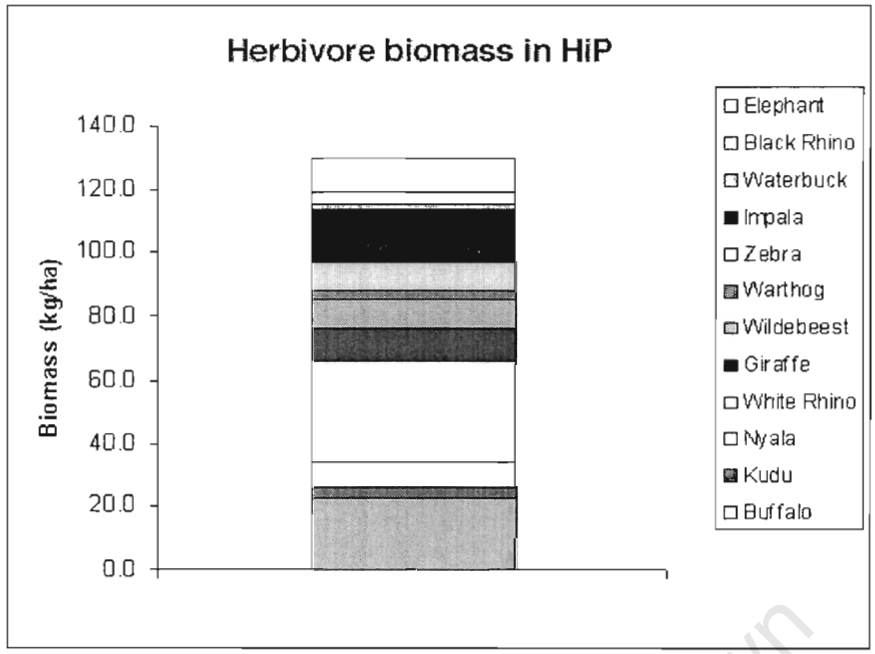


Figure 2.4. The contribution to herbivore height of the most common species of herbivores in HiP

History

The area that today includes the reserve was originally occupied by nomadic khoi-san 'bushmen', evidence of their presence still remaining in the form of cave paintings. Despite being a largely nomadic group it is likely that, as with other pre-iron age people they possessed a skilled use of fire for the purposes of hunting and attracting game and modifying their environment (Pyne 1982, Lewis 1989, Price and Bowman 1994, Whitehead et al. 2003, Bowman et al. 2004). Nguni tribes began arriving in the area from the north around the 3rd century AD (Hall 1978). They had a more settled existence characterised by the tending of cattle and the farming of maize. Extensive archaeological sites in the park remain well preserved and include kraals and iron smelting sites, indicating that the area was continuously worked and habited (Hall 1984). From 1818 the area was ruled by King Shaka who forged the disparate tribes of the area into the Zulu kingdom. He proclaimed the area between the two Umfolozi rivers as a royal hunting ground and this was likely the first form of protection that wildlife in the area experienced. It was during this period that European settlers and traders first came through the area and provided some of the early records of game in the area. The rinderpest epidemic swept the area in 1898 and this combined with malaria and nagana kept many of the lower lying areas, including Umfolozi, sparsely populated. Public concern in the late 19th century concerning the dwindling numbers of game, particularly the two species of Rhinoceros that inhabited the area, led to the proclamation of

Hluhluwe and Umfolozi (then two separate reserves) in 1897, making them among the oldest of proclaimed reserves in Africa. The area between the two reserves (known as the corridor) was proclaimed as state land in 1950 from which time the two reserves were managed together as one unit. The corridor region was officially incorporated into the reserve in 1982. The reserve was fenced in the late 1960's (Brooks and Macdonald 1983).

Of historical note it is worth mentioning the nagana campaigns which took place in and around the reserve intermittently between 1919 and 1954. Nagana (trypanosomosis) is a blood borne disease related to human sleeping sickness that effects cattle, horses and other domestic animals. Wild game, though largely immune to the disease, was thought to act as a reservoir of the blood parasite which was then passed to cattle by tsetse flies (*Glossina* spp). In order to eradicate the disease it was decided to cull all game within the reserve. It is estimated that during this period 96,000 head of game were shot within the reserve. Of this figure 70,000 head of game were shot in the years 1942-50 alone (Vincent 1970, Brooks and Macdonald 1983). Fortunately Rhino of both species were spared this slaughter due to their rarity at the time. By the end of the culls zebra and wildebeest were absent from Umfolozi (subsequently repopulating from Hluhluwe) and impala and other large herbivores were rare. Nagana was eventually brought under control only through the use of flytraps and the extensive aerial spraying of DDT, which was applied to the reserve from 1948-51. Further culling was carried out during the period 1959-70 due to concerns expressed about overgrazing of the veld and to simulate the effect of absent predators. These culls focused on short grass grazers, such as warthog, thought to compete with White Rhino for food. From 1979-84 20,000 head of both grazers and browsers were removed during a drought in order to protect the veld and prevent starvation (Emslie 1984, Walker et al. 1987).

Historically Zululand was home to sizeable herds of elephant. Ivory was exported from Delagoa Bay in Mozambique in huge quantities. The last elephant in the province, a lone bull, is recorded as having been shot in 1916 (Vaughan-Kirby 1916) though they are generally stated as having disappeared by the 1870s. Elephants were reintroduced to HiP from Kruger national park in 1979. The motivation for re-introduction was to re-establish natural processes in the park that were formerly driven by elephants. It was thought that the bush encroachment phenomenon may have been a consequence of the absence of elephants. However despite numbers increasing to more than 300 in recent years any impact on bush encroachment has yet to be seen.

The above history, though brief and highly condensed, serves to illustrate that despite having a long history of protection Hluhluwe iMfolozi has been substantially

impacted by the activities of man. For a more detailed account reference should be made to some of the following texts: (Vaughan-Kirby 1916, Vincent 1970, Feely 1978, Brooks and Macdonald 1983, Emslie 1984).

3 Grass responses to herbivore exclosures

Introduction

In this chapter I examine the factors controlling the distribution of grazing lawns within HiP and try to identify whether a top down process, grazing by various species of herbivores, is responsible for the patterns seen within the grass layer. If grazing is responsible for determining the type of grass community present is this is a general effect of all grazers? Or do White Rhino have a larger effect than other species? Bottom up processes have been previously seen to have little effect in determining grazing lawn distribution in HiP as rates of nutrient cycling, nutrient levels and soil type did not appear to correlate with grassland type (Swemmer 1998) This marks a significant way in which lawns in HiP appear to function differently from those described from the Serengeti by McNaughton.

As grazing lawns have a low standing biomass may also prevent the spread of fire. They hence have the potential to act as natural fire breaks in the landscape if they occur at a scale large enough to impede the progress of a fire. I wanted to investigate what effects the various grazing animals could have on fire through the action of their grazing. Fire and grazing animals can be thought of as both competing a shared resource; grass. I wanted to investigate if grazing animals could exclude fire from the landscape and, if so, which species of grazers are most important? Also whether any observed effect of grazers on fire occur at both high and low rainfall ends of the park?

Methods

The questions addressed in this chapter formed part of a larger project, the Zululand Grass Project (ZLGP) begun in 1999. Ten research sites were established throughout the HiP. 5 sites were in Hluhluwe and were spread across an apparent grazing gradient from tall bunch grass sites, through mixed bunch and lawn grass sites to pure lawn sites and finally to an 'overgrazed' site dominated by forbs, (this gradient was inferred from the grassland state at the time the experiment was set up and later confirmed from dung count data). Another 5 study were sites similarly situated along a grazing gradient in Umfolozi, the two sets of study sites being intended to give an insight

into the effects of rainfall as Umfolozi is a semi arid savanna and Hluhluwe a mesic savanna. Figure 3.0 shows the location of study sites in the park.

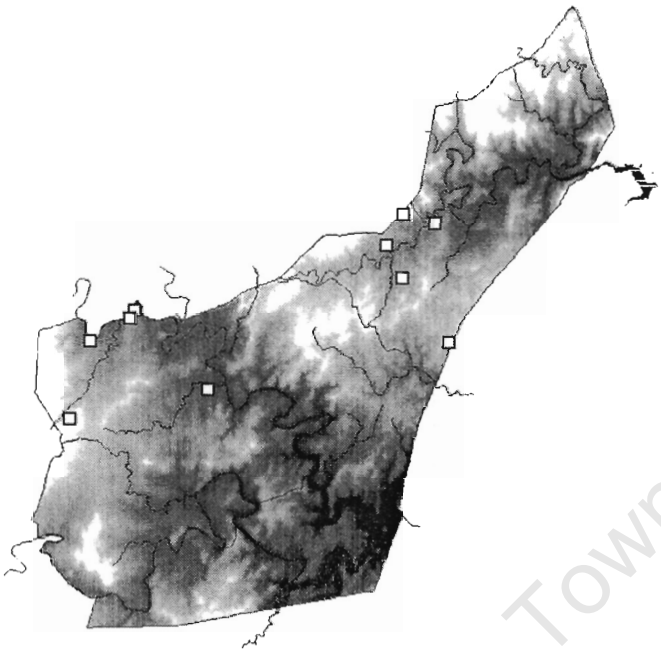


Figure 3.0. Map of Hluhluwe iMfolozi Park showing the locations of the ten ZLGP study sites (squares). Shading indicates relief

At each site three fenced exclosure plots, each roughly 40 by 40 meters were established. Plots were assigned to one of three treatments. These were the 'total exclosure' (or hare fence), which was a 2m tall game fence with a lower strip of chicken mesh designed to exclude all animals down to the size of a hare. The 'Rhino fence' (or partial exclosure) was a thick cable strung 50 cm from the ground that excluded both species of Rhino (which are unable to lift their feet far off the ground). Finally an unfenced control plot was added. This arrangement of fences is illustrated in figure 3.1. In Hluhluwe a further two fences were added by the SABRE project (University of Groningen) to each of the sites in 2000. These were the Impala fence and the Zebra fence. I excluded the zebra and impala fences from the analyses described in this chapter, unless specifically stated otherwise, because comparisons could not be made with equivalent fences in Umfolozi.

Grass height and species

In each fence a permanently marked grid was laid out marked by large nails topped with metal washers. This grid system occupied half of the area within each plot, the other half plot being used for grass clipping and other destructive experiments so that

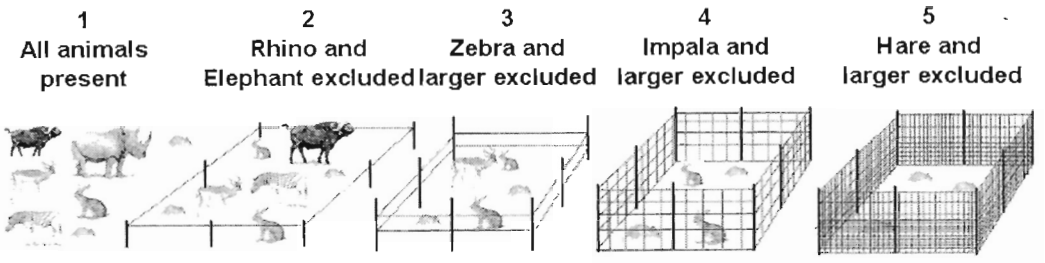


Figure.3.1. The experimental design of the ZuluLand Grass Project (ZLGP). Treatments progressively exclude herbivores of smaller size. This design was replicated at ten sites in HiP. Fences 3 and 5 were only present in Hluhluwe.

the grass layer in the marked plots remained undisturbed. Each grid consisted of 2 x 2 m squares arranged in 20 rows with 10 columns giving a total of 200 grid squares in each treatment at each site although there was some variation in number of grid squares due to variation in fence size. Grid squares were relocated by stringing ropes across the plots in line with the grid rows and then using a metal detector to find each nail. A co-ordinate system was designed to ensure the accurate relocation of grid squares. All data collected on this grid was stored in a specially designed Access database. Grass height readings were taken in the middle of each grid square with a Disc Pasture Meter (Bransby and Tainton 1977). The DPM readings have been calibrated by plotting them against actual values of biomass obtained from clipping experiments (see appendix 1). Grass species composition was recorded as the three most dominant grass species under the disc. Surveys of the grass layer were conducted annually towards the end of the growing season, usually in April/May, depending on the rainfall in that year. The first survey was conducted in 2000, giving, at the time of this thesis, four years of data. Additional surveys were also carried out on an ad-hoc basis where necessary such as before experimental burns (see below).

I analysed the variation in grass height across and between the sites in the following manner. As a preliminary investigation I calculated the median grass height for each year in each fence. This was in order to reduce pseudo-replication in the data set (the many data points in each fence are not independent of each other due to spatial auto-correlation). I analysed data from the sites in Hluhluwe and Umfolozi separately. Replicates were provided by data from the different years and the five different sites at each end of the park, effectively ignoring the grazing gradient between sites. I then performed an ANOVA and tested for differences in the mean values with a *post hoc* Tukey Kramer HSD test in the statistical analysis package JMP 5 (SAS Institute). The

data was also checked for unequal variance using a combination of Brown's, O'Brien's and Forsythe's test.

The simple averaging of data points in each fence leads to a considerable loss of information in the data set as each sample of 200 data points is reduced to a single value. In order to perform a more detailed analysis I classified the DPM readings in each fence in to one of two categories based on height. These classes were short grass (less than or equal to 5cm DPM) and long grass (greater than 5cm DPM). The proportion of each grid occupied by short grass was then calculated for each fence for each year of data.

This summary data set was entered into a general linear model (GLM) in JMP. I constructed two models: one for Hluhluwe and one for Umfolozi. The variables site, year and fence were entered as predictor variables and were crossed in order to examine potential interactions between factors. Finally I drew bar graphs indicating the amount (proportion) of short grass in the three treatments at both ends of the park. Sites were arranged along the aforementioned grazing gradient.

To determine whether the removal of grazing had led to any increase or decrease in grass species diversity, I counted all identified grass species in each fence at each site for each year of the study. In order to test for changes in species composition within the experimental plots I scored the two dominant grass species under the disc with a value of 2 and the third dominant species, if present, with a value of 1, where dominance is measured by cover. (In my experience there was often little difference in the amount of the first and second most dominant grasses under the disc). Scores for each year were summed for each grass species in each fence at each site. I then took data for the 15 most common grasses for further analysis and performed two analyses on this data set. The first analysis compared scores for each grass in each fence at each site for the years 2000 and 2003. This was a matched pairs analysis in JMP (equivalent to a paired T-test), and was designed to detect any change in the species composition over the period of the study. Secondly I compared the scores for each grass in the total exclosure and in the Rhino fence to the score for that grass in the control plot for each site in 2003. This was designed to test for any change in grass composition that had resulted from 4 years of the various grazing exclusion treatments.

Dung

At the end of each calendar month a permanent marked transect 20m in length was walked within each fence and in the control plot at each site. Along this transect the number of dung or dung piles were counted in a strip two meters on either side of the transect. Dung was marked with coloured tooth picks so that it was not re-counted in subsequent months. All data was entered into an Access database before it was analysed. Because I were primarily interested in the effects of White Rhino grazing upon other species, I compared the amount of dung found in the control plot to the amount of dung found within the Rhino fence (very little dung was found within the total exclosure). I initially performed a matched pairs analysis in JMP to test for differences in the amount of dung deposited in the two treatments during each month. Again this test is equivalent to a paired t-test. I first considered all sites separately and then grouped the sites at the two ends of the park together to increase the sample size. This analysis was performed for each of the main species of grazers. The paired T-test does not test for direction of effect or long-term trends but only for significant differences in each pair of data points. I also plotted graphs showing the difference in the amount of dung between the control plot and the Rhino fence against time and fitted these with regression lines to see if there were any obvious trends in the data series. I restricted this latter analysis to Impala dung as it was most numerous and would hence show any long-term trends most clearly. Sites from the opposite ends of the park were grouped together.

Fire

Experimental fires took place three times, in the years 2000, 2002 and 2004. The spread of fire was measured on the same 2 by 2 meter grid used to measure grass height and species. Before the fire grass height (but not species) was measured using a disc pasture meter. After the fire the grid was resurveyed to obtain a burn value for each grid square. Each square was measured on a scale as follows: 0= No burn, 1=Partial burn, 2= complete burn.

All data was entered from the field sheets in to the Access database from which data was extracted for analysis. Firstly I plotted the mean burn score against each half-centimetre increment of DPM reading in order to determine the relationship, if any, between grass height and grass combustion. This analysis did not look at fence effects and so included data from burns in the impala and zebra fences in Hluhluwe in order to increase sample size.

Secondly in order to see if there was a relationship between the spread of fires and the proportion of tall grass present in each fence, I plotted the proportion of each treatment plot that burnt (i.e. had a burn score of 1 or 2) against the proportion of tall grass (>5cm DPM) present. Again this analysis included data from both the zebra and impala fences.

Finally I plotted the difference between the percentage area burnt in the control and Rhino fences for all sites in Hluhluwe and Umfolozi to determine the relative effect of Rhino and other grazing species on fire spread. This data was summed across all years. In this analysis I chose not to use the extra fences in Hluhluwe as they could not be replicated in Umfolozi.

Results

Grass height

Initial sample size was 30,827 data points over a period of 4 years (2000-2003). This sample was reduced to 120 by calculating averages (median) for each treatment at each site for all the years for which data was available. Table 3.0 presents the results of the initial T-test performed on averaged DPM readings from each fence. I tested for unequal variances in the data but found none. Figure 3.2 gives a simple graphical representation of these results. Note that the mean values of grass height for the control and exclosure plots are not that dissimilar in Hluhluwe and Umfolozi, with grass height in Hluhluwe being consistently slightly higher. However the mean grass height in the Rhino fence is much closer to that of the control plot in Umfolozi than it is in Hluhluwe. The results of the general linear model (GLM) are given in table 3.1. It can be seen that the R-square of each of the models is over 90% indicating that the models explained a high degree of the variation present in the data. The individual predictors **fence** and **site** were highly significant in each of the models constructed. They also explained most of the variation in the data as is reflected in values for the sum of squares. The predictor term **year** was also highly significant in Hluhluwe, where it accounted for a lot of the variation in the amount of short grass, but was not significant in Umfolozi. The interactions between **site** and **fence** and **fence** and **year** were also significant in Hluhluwe and **site*year** was significant in Umfolozi. Other interactions between terms were generally less important both in terms of significance and amount of variability accounted for. I also arc-sine transformed the data to check the test had not been invalid because of skewed data but this had no effect on the results of the GLM. Figure 3.3 gives a visual representation of the effect of grazing pressure on the amount of short grass at each site.

It clearly shows how the fence effect differs according to the grazing pressure at each site. R-squares of the fit of each line are also given.

Table 3.0. Comparison of test statistics for the averaged grass height. Grouping indicates the results of the post *hoc* Tukey Kramer HSD test. Samples not sharing the same letter are significantly different at the p=0.05 level. Fence Ex= total exclosure, Pa=Rhino fence and Co=control. N=sample size, grass height is measured as the settling height (cm) of a disk pasture meter.

park	Fence	Grouping		N	Mean	Lower 95%	Upper95%
Hlu	Ex	A		20	27.3	22.6	32.0
Hlu	Pa	A	B	20	20.8	16.1	25.5
Hlu	Co		B	20	13.6	8.9	18.3
Umf	Ex	A		20	24.5	21.5	27.6
Umf	Pa		B	20	12.4	9.3	15.4
Umf	Co		B	20	10.2	7.1	13.2

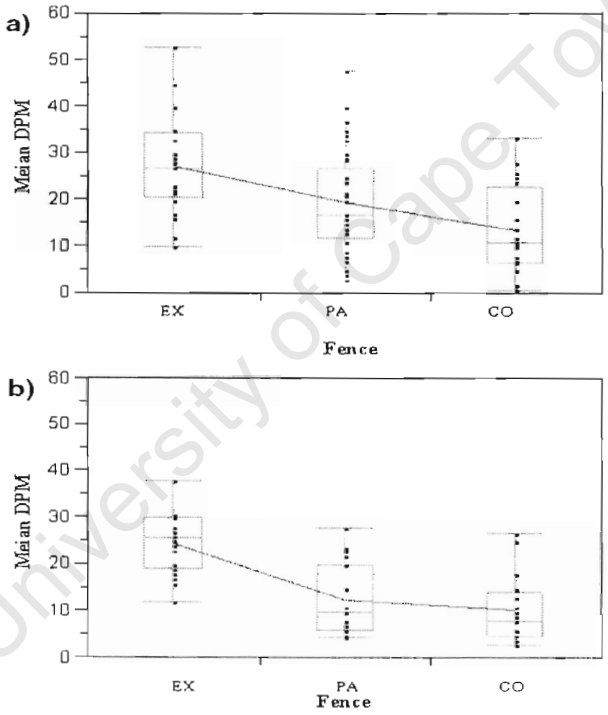


Fig 3.2. Graph of the mean DPM (cm) for each treatment in a) Hluhluwe and b) Umfolozi. CO = all herbivores present, PA, = Rhinos excluded, EX = all herbivores excluded. Line connects means. Centre line of boxes indicates median value, boxes 25% and 75% quantiles.

Table 3.1. Results of a general linear model constructed with the proportion of short grass in each fence as response variable. Separate models were constructed for a) Hluhluwe and b) Umfolozi. The R-square for each model is given followed by the 3 terms used as explanatory variables which are also crossed. Reported statistics include the sum of square for each term (i.e. the relative amount of variation explained) the F statistic and the probability of the F statistic being met by chance alone. Probabilities of <0.05 are marked in bold.

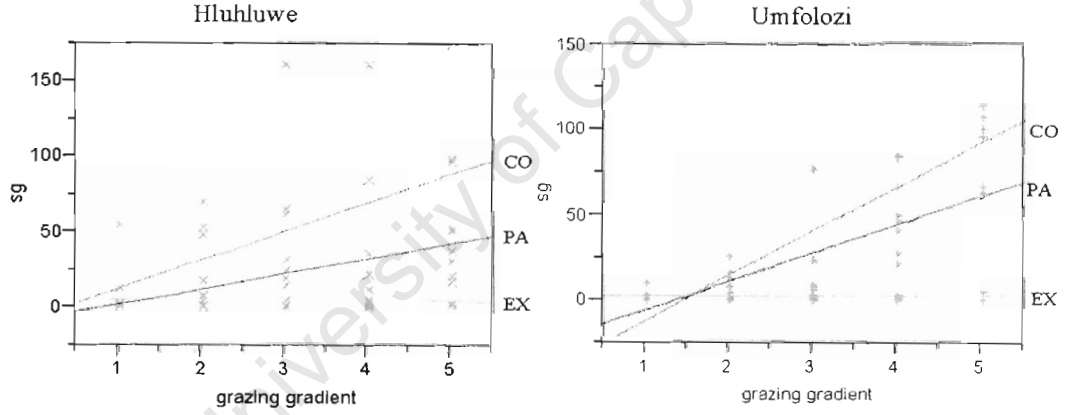
Proportion Short Grass

a) **Hlu**

R Square		0.95		
term	**DF**	**Sum of sq.**	**F**	**Prob>f**
site	4	12083.8856	14.7191	**<0.0001**
fence	2	21093.8804	51.3880	**<0.0001**
site*fence	8	9662.8720	5.8851	**0.0003**
year	3	33122.2638	53.7940	**<0.0001**
site*year	12	5323.4837	2.1615	0.0522
fence*year	6	12760.5050	10.3622	**<0.0001**

b) **Umf**

R Square		0.94		
term	**DF**	**Sum of sq.**	**F**	**Prob>f**
site	4	27427.0548	40.4575	**<0.0001**
fence	2	15709.2432	46.3452	**<0.0001**
site*fence	8	17388.4075	12.8248	**<0.0001**
year	3	329.3770	0.6478	0.5920
site*year	12	6039.1273	2.9694	**0.0112**
fence*year	6	1704.9379	1.6766	0.1701



R-square

Fence	Hlu	Umf
co	24.2	70.2
ex	0.1	0.3
pa	24.6	61.4

Fig 3.3. The number of grid squares with short grass (<5cm) from a total of 200 within each treatment. Lines fitted to points from each fence, N=4 (years) in each case. Sites are arranged along a grazing gradient as follows (Hlu/Umf): 1=Maquanda/Sokwasela, 2=LeDube/Gqoyeni, 3=Klasana/Thobothi, 4=Nombali/Mbusane, 5=Seme/Mona. Grazing intensity increases from left to right. CO = all herbivores present, PA, = Rhinos excluded, EX = all herbivores excluded. R^2 is the % variance explained by the linear regressions.

Grass Species

There were 64,878 records of 34 species of grass found at all sites in the 4 years of data available. Figure 3.4 indicates that there was very little change in the total number of species found in the treatments over the years of the study. What is more the number of species did not appear to be markedly different between treatments, although there were generally more grass species at sites in Hluhluwe. However this does not indicate that no species turnover occurred during this period. Table 3.2 shows the results from comparing individual species scores from the years 2000 and 2003 in each fence. Species scores were summed to the level of park and comparisons were made using a matched pairs analysis in JMP (equivalent to a paired T-test). Table 3.3 gives the results of a similar paired analysis performed by comparing the grass species scores in the control to those in the Rhino fence and the exclosure. Data comes solely from 2003.

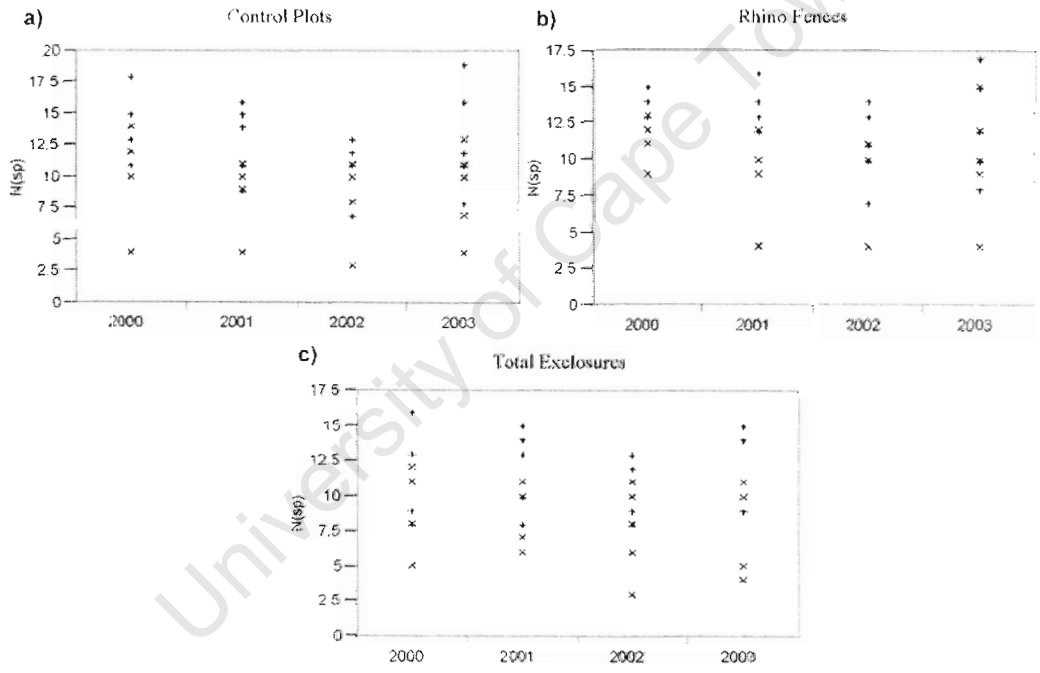


Fig 3.4. The number of different grass species counted in the four years of the study in a) Control plots, b) Rhino fence and c) Total exclosure. Diagonal crosses indicate sites in Umfolozi and horizontal crosses mark sites in Hluhluwe.

Table 3.2 Comparison of the species scores for selected grasses in 2000 and in 2003 using a paired T-test. Values given are probabilities; those marked in bold are significant at the <0.05 level. Arithmetic sign indicates the direction of shift with a plus sign indicating an increase from 2000 to 2003; N/A indicates a sample size too small to perform the test adequately. Species codes: TT= *Themeda triandra*, DL= *Digitaria longiflora*, PM= *Panicum maximum*, SP= *Sporobolus pyramidalis*, PC= *Panicum coloratum*, UM= *Urochloa mosambicensis*, BI= *Bothriochloa insculpta*, DE= *Digitaria eriantha*, ES= *Eragrostis superba*, EC= *Eragrostis curvula*, SN= *Sporobolus nitens*, AO= *Aristida congesta*, DA= *Digitaria argyrograpta*, HC= *Heteropogon contortus*, CG= *Chloris gayana*,

	HLU			UMF		
species	Exclosure	Rhino fence	Control	Exclosure	Rhino fence	Control
TT	0.0625 +	0.2267 -	0.3018 +	0.2139 +	0.0463 +	**0.0177** +
DL	0.1060 +	0.0690 +	0.0562 +	N/A	N/A	N/A
PM	0.3866 -	0.7551 -	0.7839 -	0.2876 +	0.8652 +	0.9199 -
SP	0.7438 +	0.5208 +	0.3111 -	N/A	N/A	N/A
PC	0.5620 +	0.1845 -	0.5658 -	**0.0416** -	0.2246 -	0.2595 -
UM	N/A	N/A	N/A	**0.0264** -	0.9153 -	0.5297 -
BI	0.0812 -	0.0535 -	**0.0232** -	0.0979 -	0.2051 -	0.1847 -
DE	0.3442 +	0.4124 +	0.2979 +	0.1614 +	0.2746 +	0.3990 +
ES	0.1046 -	0.2126 -	0.1499 -	0.6903 +	0.8057 -	0.2340 -
EC	0.5100 +	0.9175 +	0.5899 +	0.1853 +	0.0983 +	0.2522 +
SN	0.5000 +	0.4291 +	0.3454 +	0.2952 -	0.1647 +	0.1621 +
AO	N/A	N/A	N/A	0.2504 -	0.7208 +	0.9752 +
DA	0.6035 -	0.8846 +	0.6088 -	0.5000 +	0.3440 -	0.5335 +
HC	0.4166 -	0.5949 -	0.4010 -	0.5552 -	0.5508 -	0.5352 -
CG	0.6903 -	0.1211 -	0.8889 -	N/A	N/A	N/A

Table 3.3. Comparison of a matched pairs analysis comparing species scores in the Rhino fence and the exclosure to species scores in the control. Data comes solely from the year 2004. Values are probabilities from a paired T-test and the arithmetic sign indicates the direction of the effect with a minus sign indicating a higher score in the control plot. Species codes are as given for table 3.2.

	HLU		Umf	
species	Exclosure	Rhino fence	Exclosure	Rhino fence
TT	0.7860 -	0.5546 -	**0.0075** +	0.7899 +
DL	0.4286 -	0.9589 +	N/A	N/A
PM	0.0972 -	0.2230 -	0.4050 -	0.1154 -
SP	0.5279 -	0.4216 +	0.5000 -	N/A -
PC	0.2821 +	0.5666 -	0.4915 +	0.3661 +
UM	0.4226 +	0.3964 +	0.8301 -	0.1868 -
BI	0.0772 -	0.7498 -	0.3902 -	0.8711 -
DE	0.1984 +	0.1850 +	0.9423 +	0.1457 -
ES	0.3934 +	0.1159 +	0.9293 +	0.6788 +
EC	0.6310 -	0.9038 -	0.3705 -	0.4596 -
SN	0.1682 -	0.2811 +	0.6070 -	0.1696 +
AO	N/A	N/A	0.6485 -	0.2407 +
DA	0.7040 +	0.3244 +	0.5299 -	0.4502 +
HC	0.9651 +	0.5573 +	0.7311 -	0.4679 +
CG	0.1926 +	0.2433 +	N/A	N/A

Dung

A total of 4903 records of dung from 23 species of mammals were recorded between December 1999 and October 2004 at the ten sites. Results from the matched pairs analysis comparing the amount of dung in the control to the amount of dung in the Rhino fence each month is given in table 3.4. Results are given separately for each site and then with data grouped at both ends of the park. Figure 3.5 shows the trends in impala dung over time for sites at both end of the park. Fitted linear trend lines were flat indicating no long terms trends.

Table 3.4. P values for matched pairs analyses comparing differences in the amount of dung in the control versus the Rhino fence for various species of grazers. Test statistic is equivalent to a paired T-test. Statistics significant at less than 0.05 are highlighted in bold. Tests are done separately for each site (marked 1-5 along a grazing gradient with 1 as the site with the least amount of grazing and 5 having the most grazing pressure), and then with the data from each site summed together to the level of park, (column marked sum). 1=Maquanda/Sokwasela, 2=LeDube/Gqoyeni, 3=Klasna/Thobothi, 4=Nombali/Mbusane, 5=Seme/Mona.

IMPALA	1	2	3	4	5	Sum
Hluhluwe	0.8064	0.3049	0.0639	**0.0370**	**0.0142**	0.0649
Umfolozi	0.2845	0.2193	0.1114	0.9923	0.1119	**0.0069**
WILDEBEEST	1	2	3	4	5	Sum
Hluhluwe	1.0000	0.2235	0.4123	**0.0029**	0.1108	**0.0009**
Umfolozi	0.4650	0.3287	0.9513	0.0650	0.3431	0.2327
BUFFALO	1	2	3	4	5	Sum
Hluhluwe	0.1495	**0.0009**	**0.0020**	**<0.0001**	0.1454	**<0.0001**
Umfolozi	**0.0009**	**0.0002**	0.0009	0.1778	**0.0133**	**<0.0001**
WARTHOG	1	2	3	4	5	Sum
Hluhluwe	0.7234	0.5565	**<0.0001**	0.2275	0.8704	**<0.0001**
Umfolozi	**0.0243**	0.3181	0.7370	**0.0079**	0.4071	**0.0827**
ZEBRA	1	2	3	4	5	Sum
Hluhluwe	**<0.0001**	**0.0020**	**0.0005**	**<0.0001**	**0.0033**	**<0.0001**
Umfolozi	**0.0133**	**0.0029**	**0.0013**	0.1838	1.0000	**<0.0001**

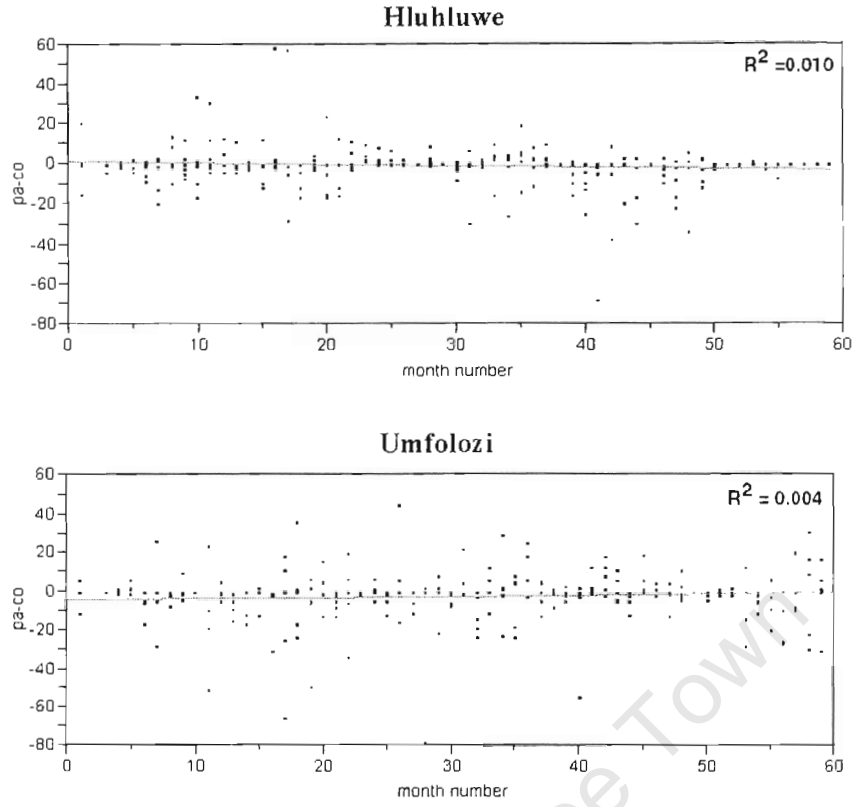


Figure 3.5. Graph of the difference in the amount of impala dung between the control and Rhino fence (pa-co). Units are number of separate dung piles. Sites at the different ends of the park are grouped together. Values on the x-axis are the month number of the study. Month 1=Dec.99 and Month 60= Oct. 04. The line is a fitted linear trend line and the value in the upper right the degree of fit (R-square) of this line.

Fire

In total there were 21,200 data points covering experimental burns from three years at each of the ten different ZLGP sites. Each data point represents a pair of data points giving values for pre-burn grass height and burn score. Figure 3.6 shows a plot of DPM against average burn value. This was used in order to ascertain whether there was a consistent minimum combustible grass height. From this graph it was estimated that below a DPM value of 5 cm it was unlikely that the grass in a grid square would burn. I used this value of 5cm as a cut off between two classes of grass termed 'long' and 'short', which were used in the calculations to produce figure 3.7. Figure 3.7 shows that a minimum amount of 'long' combustible grass is needed for fire to move through a plot. This amount is somewhere between 50 and 60 % long grass, below which no plots were able to burn at all. Above this value most plots burnt completely although there is some amount of scatter in the data points indicating incompletely burnt plots.

Finally figure 3.8 shows the result of comparing the area of a plot that burnt in the Rhino and control fences. Vertical bars represent the difference in % area burnt between the Rhino fence and the control plot and is a measure of the effect of excluding Rhinos on the spread of fire. Negative values indicate that the area burnt was greater in the Rhino fence. Data is averaged for three years of fires.

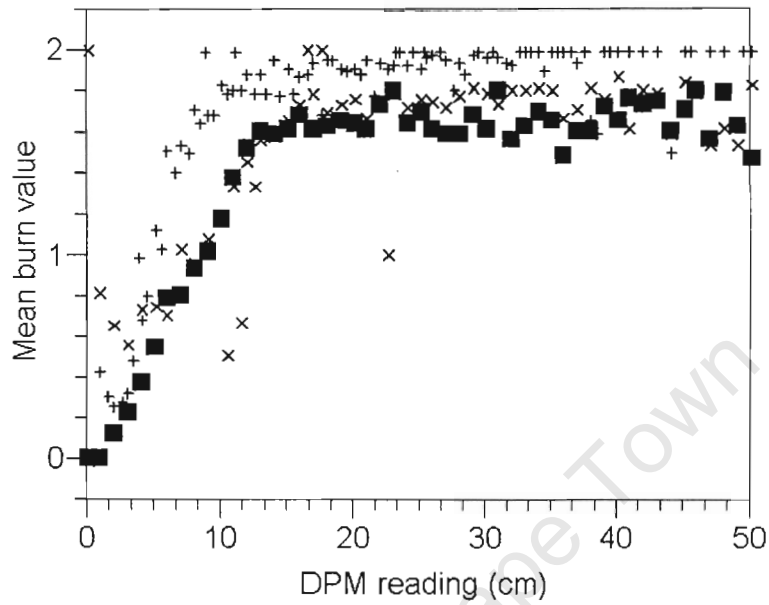


Figure.3.6. Average burn value (where 0=no burn, 1=partial burn and 2=completely burnt) plotted against DPM. Diagonal crosses indicate fires that too place in 2000, straight crosses are fires that took place in 2002 and filled squares are fires that took place in 2004.

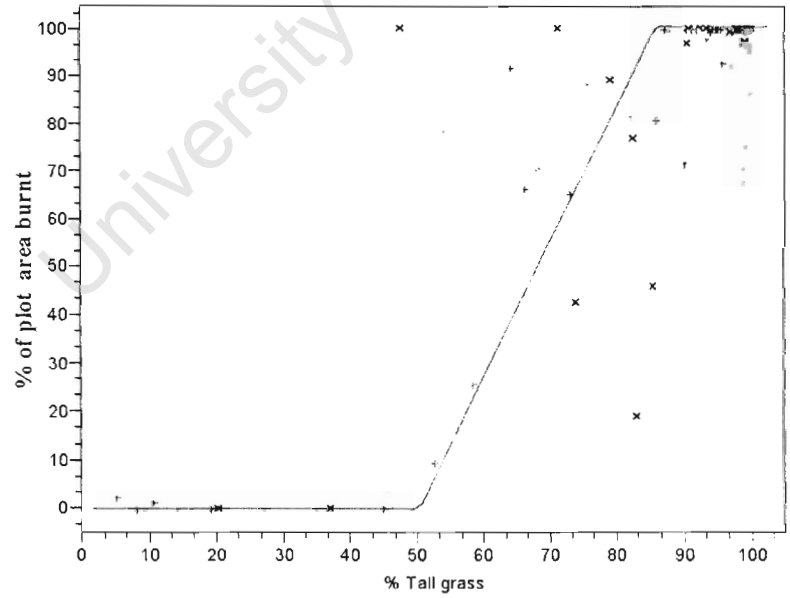


Figure 3.7. The percentage of grid squares within a fenced plot that burnt (y-axis) plotted against the % of tall grass (>5cm DPM) in that plot (x-axis). Symbols indicate different years as defined for figure 3.6. The line is hand drawn and is purely for illustrative purposes.

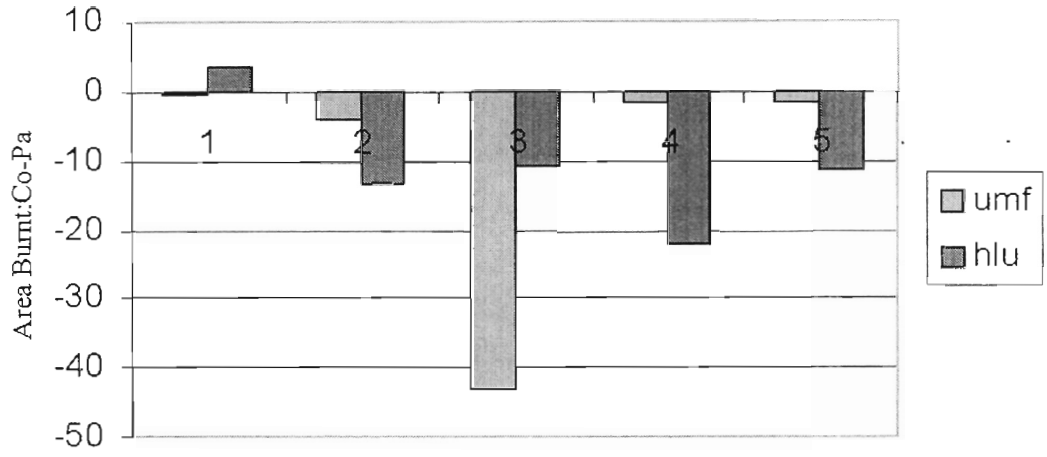


Figure. 3.8. The difference in area burnt between the Rhino fence (Pa) and the control (Co). Values are summed for each site across all years. Negative values indicate a greater area burnt within the Rhino fence. Numbers along the X-axis represent the grazing gradient between sites (1=Maquanda/Sokwasela, 2=LeDube/Gqoyeni, 3=Klasana/Thobothi, 4–Nombali/Mbusane, 5=Seme/Mona.)

Discussion

Grass height and species

The effect of grazer exclusion on grass height can clearly be seen both in Hluhluwe and Umfolozi. In both cases grass height was significantly higher within the total exclosure compared to the non-fenced control. However the effect of excluding Rhino differed between the two ends of the reserve. In Hluhluwe grass height within the Rhino fence was significantly different from neither the control or the total exclosure. In contrast, in Umfolozi, grass height was similar in the control and the Rhino fence but both had much less grass than the total exclosure. This would appear to indicate that other species of grazers can replace the effect of White Rhino grazing in Umfolozi but in Hluhluwe other grazers cannot compensate for the effect of White Rhino exclusion.

The second point to note is that grass height is generally higher in Hluhluwe than in Umfolozi, presumably as a result of the higher rainfall in Hluhluwe. It would appear that in Hluhluwe the smaller bodied grazers cannot cope with the higher grass growth rates that result from higher rainfall as well as the megaherbivore.

These trends were largely confirmed by the GLM. The variables 'site' and 'fence' both explained a large amount of the variation in amount of short grass between plots and are highly significant. Hence the fence effect described above is confirmed. The fact that there seems to be as much inter-site variation in height as there is intra-site variation (i.e. between treatments) can be explained by the fact that sites were situated

along a grazing gradient from tall to short grasslands. Hence the effect of removing grazing pressure via the construction of a fence is expected to be smaller at a site with low grazing pressure than at site with high grazing pressure, i.e. at a site with a grazing lawn. This is easily seen in figure 3.4. It can clearly be seen how the effect of grazer exclusion increases with higher grazing intensity. It is this variation that is being coded for in the GLM by the variable 'site'.

The term 'year' also had a significant effect on height, particularly in Hluhluwe, where it explained a greater amount of variation than either fence or site. In this analysis the term 'year' is also a proxy for inter-annual variation in rainfall. In Umfolozi year (=rain) explained much less of the variation in grass height. The remaining interaction terms were generally weaker and less significant than the individual terms. The high level of fit (R-square) exhibited by these models indicated that although there were relatively few predictor variables they were sufficient to cover almost all the variation in the data set.

The pattern of change in grass species was much less clear. Very few of the grasses shown in table 3.2 showed a significant increase or decrease between the years 2000 and 2003. *Panicum coloratum* and *Urochloa mosambicensis* showed a decrease within the total exclosure but this effect was only apparent in Umfolozi. *Themeda triandra* also appeared to increase in the control plot in Umfolozi, contrary to our expectations. The only grass to show a significant change of score in Hluhluwe was *Bothriochloa insculpta*, which decreased within the control plot. The fact that many of these changes occurred in the control plot, which should theoretically show the least change, illustrates the dynamic nature of savannas but also the effects of inter annual variation in rainfall. Table 3.3 does not clarify this situation much, producing only one significant result, that of *T. triandra* which was seen to be significantly more abundant in the exclosures of Umfolozi with respect to the control plots. This result at least was in the direction expected with exclusion of animals leading to an increase in bunch grass. However it is odd that no significant decreases in other species of grass, particularly lawn grasses were detected by this analysis. .

It is clear from these analyses that the exclusion of White Rhino does have an effect on grass height. However this effect is far more pronounced in Hluhluwe which has a higher annual rainfall. This effect appeared quite rapidly after the construction of the fences and was already evident by the time of the first survey in 2000, a period of only 9 months. This represents a structural change in the grass layer. However no

equivalent evidence for a compositional shift in grass species can be seen which is surprising given the amount of time over which the experiment has taken place.

Dung

The matched pairs analysis shows that there were some significant differences between the amount of dung in the control plot and Rhino fence at some sites for some animal species. Impala and wildebeest show significant differences at some of the more heavily grazed sites in Hluhluwe. Many of the larger grazers also show significant effects. However I believe that fence effects on animal exclusion come more into play with the larger species of grazers as they are less likely to cross the fence. Figure 3.5. shows that despite the above results there were no consistent trends (e.g. more dung in the Rhino fence) and that points were evenly distributed above and below 0 on the y-axis. The fitted line is centred on zero indicating that although significant differences were found for individual months, there was no overall trend between months. Furthermore there were no long-term trends, either an increase or decrease in dung in any of the fences or evidence for annual cycles that may be related to annual variation in rainfall. There is a large degree of variation in the amount of scatter around the y-axis and it is possible that this could be related to variation in timing of rainfall. Further analysis may yet elucidate some relationship between dung deposition and rainfall.

Fire

It can clearly be seen from figure 3.6 that there was a consistent relationship between the height of grass in a grid square and its chances of burning. This seems to state the obvious as a fire cannot burn without sufficient fuel. From this graph I extracted a value of 5 cm DPM to use as a cut off point, below which there is a relatively small chance of fire moving through a grid square. (However any grid square that has a grass height greater than 5cm DPM is highly likely to burn). The data appears to be remarkably consistent despite the fact that individual fires occurred on different days and hence burnt under different conditions of air temperature, humidity, wind speed and fuel moisture content. Although the shape of the plots for the different years remained very similar there was some small amount of variation in the position of the curves with data for 2004 appearing to be placed slightly to the right of the other curves. Variation between years is likely to be caused by variation in rainfall in the months before the fires affecting the overall grass height and fuel moisture.

Figure 3.7 also shows a relationship that appears to be consistent not only between different fires in the same year but also for fires occurring in different years. Again it appears that there is a lower limit below which fire is unable to spread. The cut off point appears to be somewhere around 60% tall grass. Below this value none of the plots burnt whilst above the value almost all of the plots burnt completely. The slight scatter of points >60% long grass is likely to reflect the effects of weather on the day of the fire and also of fuel moisture on the spread of fire. It is perhaps surprising how consistent this relationship appears to be when these factors are taken into consideration. Measurements of fire intensity and rate of spread taken from the same fires show a large amount of variation between fires that is strongly correlated with local weather conditions and fuel moisture content. However it appears, at least on the small scale of the ZLGP experimental sites, that the area burnt is solely determined by the amount and distribution of grass biomass.

Figure 3.8 shows that, with one exception, there is little difference in the area burnt between the Rhino fence and the control at the sites in Umfolozi. This would indicate that grazing animals other than White Rhino could have an effect on fire spread in Umfolozi that is equal to that of a White Rhino. In Hluhluwe however there is a difference in the area burnt in the rhino fence and the control plot suggesting that in Hluhluwe it is the White Rhino who are largely responsible for grazing grass short enough to impede the spread of fire. The one glaring exception to this generalisation is the site at Mbusane which appears to have a massive Rhino effect. This effect is consistent across years and is not the result of only one outlying data point. It is possible that Mbusane may have an unusually high number of Rhinos locally, an idea born out by a recent survey of Rhino middens (dung piles) around the ten sites, (ZLGP data).

Conclusions

It is clear that grazing animals do have a profound effect on grass height and in the structuring of grazing lawns, but it has been much harder to find an equivalent fence effect upon grass species. The Rhino fence effect appears to be much larger in Hluhluwe than it is in Umfolozi and this effect is probably related to the annual rainfall experienced at the two ends of the park. Effects of excluding Rhinos upon other species of grazers are present but the direction of the effect does not appear to be consistent and the overall picture is unclear. However there does appear to be a clear and consistent relationship between grass height and fire spread which is independent of fire weather variables. These results give indications of the functional importance that the White Rhino plays in

structuring mesic savannas and suggest explicit hypotheses that will be tested in later chapters of this thesis.

4 Development of a spatial database of White Rhino removals

Introduction

The results from the fenced exclosures discussed in the previous chapter provide interesting insights into the factors influencing the grass layer within the savannas of Hluhluwe iMfolozi Park. However it is difficult to take results from such small areas (the exclosure each occupy roughly a tenth of a hectare), and generalize them to the much larger scale of the systems operating in Hluhluwe iMfolozi Park (which occupy tens of thousands of hectares). The heart of the problem is that different biological processes occur at different scales. Hence when studying biological systems many processes only become apparent when viewed at larger scales. This problem is referred to as scaling up. Different processes (e.g. fire and grazing) can interact in complex manners and over some distance (Archibald et al. 2005) giving rise to emergent properties of their own. These emergent properties can either amplify or reduce the effects observed by studies performed at a small scale. Biological effects may be different or even opposite in different habitat types and these effects may not propagate between patches of habitat if separated by patches of other habitats (Turner et al. 2001). All of these considerations may not be apparent when studies are performed at a small spatial scale. To attempt a study which takes these factors into account is to perform that study at a landscape scale.

In order to test whether the results in chapter 2 indicate mechanisms that play a role in shaping the ecology of Hluhluwe iMfolozi Park or whether they only operate at a limited scale within exclosure plots I needed to design a landscape scale experiment to test them. My aim was to investigate whether White Rhino grazing had the same effects on fire behavior, animal usage and grass height when studied at a landscape scale as it did within the ten relatively small fenced ZLGP research sites. If these processes are occurring at a landscape scale within the park they could have important consequences for our understanding of the ecosystems contained within the park and hence for the management of these systems in the reserve.

Measuring the impact of the various species of herbivores present in savannas at a large scale is a difficult task. Usually some sort of disturbance to animal populations is required the consequences of which can then be monitored. Disturbances to animal populations can take the form of introductions, culling (Eltringham 1970) or local

extinctions. However such interventions for experimental purposes are costly and rarely ethical from an animal welfare or conservation point of view. Occasionally it is possible to use long term fluctuations in animal populations to test theories (Sinclair and Norton-Griffiths 1982). However the detailed and long-term records needed for this kind of an analysis are rare. Because of this many landscape scale experiments adopt a correlative approach being investigations of naturally occurring disturbances rather than controlled field manipulations. However in HiP just such a disturbance occurs on an annual basis in the form of the capture of White Rhino, a brief history of which is given below:

History of Rhino Capture

When the reserves were first formed in 1895 Umfolozi was the only place left in Africa where the southern sub-species of the White Rhino could be seen, though they had formerly been distributed between the Zambezi and Orange rivers with Zululand being the southern limit of their distribution (Owen-Smith 1988). In 1916 it was estimated that only 30-40 White Rhino remained in the reserve (Vaughan-Kirby 1916). However with intensive protection their numbers began to increase rapidly and by 1942 the population had risen to about 720 individuals in the whole reserve with a further rise to 1600 individuals by 1967. Their rapid population increase was no doubt helped by the lack of competition from other grazers which were scarce due to the Nagana campaigns, from which White Rhino had been exempted. It was estimated that in 1952 the White Rhino accounted for 90% of the animal biomass within Umfolozi (Vincent 1969, 1970). However there was still concern for the long-term safety of the species as it existed as a single population, vulnerable to epidemic diseases or other such catastrophes. Unfortunately there did not exist at the time the technology needed to capture and transfer White Rhino between reserves as had been accomplished with smaller species of antelope since the 1930s (Gush 2000). Populations of all animals had been rising since the end of the nagana campaigns and concerns were raised about perceived deterioration of the veld through overgrazing. Two young orphaned male White Rhino were transported to Pretoria zoo in the early 1950s. They were roped and netted before being loaded into crates for transportation. Despite being successful it is significant that these experiments were not repeated.

Several developments occurred in the late 1950s and early 60s which made possible the safe capture and transport of White Rhino. The first was the release onto the market of new drugs such as M99, a highly potent opiate 100 times more powerful then morphine. This allowed for the immobilization of Rhinos using relatively small doses.

Secondly efficient drug delivery systems became available with the introduction of reliable gas powered dart guns. After a number of trials moving White Rhino within the reserve, the first animal to be captured with these techniques was transported to the nearby Mkuse Game Reserve on the 19th of July 1961. Despite many difficulties and the death of 'Amber' (the first animal moved) from injuries sustained when the truck slid off the road and became stuck for 24 hours during transportation to Mkuse (Gush 2000), the operation was declared successful.

So began Operation Rhino, which had the stated aim of repopulating White Rhino to reserves within their former distribution range. White Rhino were transferred to Mkuse Game Reserve, Kruger National Park and other reserves in Swaziland, Botswana and Zimbabwe as well as to Zoos and other institutions overseas. In the period 1959-81 2648 White Rhino were removed from the reserve and the world wide population is now estimated to be around 11,000. White Rhino were downgraded from the CITES appendix 1 list in 1994 and their rescue from the brink of extinction is undoubtedly one of the greatest success stories that conservation has to tell.

Present day management of White Rhino in HiP

Because of their size megaherbivores are rarely affected by predation and their population is limited by food resources. Norman Owen Smith has hypothesized that they would respond to reduction in forage quantity or quality (such as might occur during a drought) by dispersing in to new areas. However as most populations of megaherbivores now exist within fenced reserves this is no longer possible and hence severe effects such as vegetation degradation can occur (Owen-Smith 1988). In order to mitigate these effects it was decided to implement a source-sink strategy for the management of the White Rhino population within HiP in the early 1980s (Owen-Smith 1981, 1983). This involves the sub-division of the reserve into a number of different zones termed 'sources' and 'sinks'. A core population of Rhino is located in the center of the reserve and this acts as a source of dispersing individuals. Rhinos in this area are not subject to any removals. The core area is surrounded by a number of sink or vacuum zones from which White Rhino are removed. In practice sink areas cannot be maintained as completely devoid of Rhinos and represent low density areas. Animals in the core area respond to food availability and social pressures by dispersing to sinks from where they are captured and removed from the population. Thus numbers of Rhino available for capture from the sink areas are determined by the prevailing conditions in the core. This strategy eliminates the need for setting harvest levels from estimates of carrying capacity and uses

the natural system to determine harvest levels. For example, the culling of animals during drought years may not be necessary as Rhinos can disperse into the sink areas.

In order to calculate the number of White Rhino that can be removed from the sink areas each year an estimate of White Rhino density is obtained in the late dry season by conducting an aerial survey of the park from a fixed wing aircraft. These are termed 'sink counts'. Transects are flown in a north/south direction with a 500m strip width (250m on either side of the plane). All White Rhino sighted, along with their position, are recorded into a computer linked to a GPS device using the software package CartaLinx (Clark Labs.) Because the survey consists of only a single flight (or sample) accurate population estimates cannot be made. However the relative densities of White Rhinos within the core and sink areas can be estimated. These relative densities are used in conjunction with data from the biennial game census (a series of replicated ground transects which employs DISTANCE sampling, a more robust method of population estimation) in order to estimate the number of White Rhino present in each of the sink areas. The park ecologist then calculates the number of White Rhino available for removal from the sinks.

The removal of such a large herbivore must presumably lead to a significant release of grazing pressure on the grass layer within its home range. A rough calculation of grazing pressure, using numbers of the various grazing species in the park in 2004 (Rensburg 2004), the average weights of the various species of grazers (Kingdon 1997) and the areas of the various sections in the park (Anon 02) shows that White Rhino account for over a third of the grazing biomass present per hectare. This figure is likely to be an underestimate for grazing pressure on lawns. Because grazers such as buffalo feed solely on long grass they do not utilize grazing lawns for feeding. Hence relative White Rhino biomass on lawns is likely to be even higher. If this is taken into account and buffalo are removed from the calculation then White Rhino account for over 50% of grazing biomass on lawns in Hluhluwe and 43% in Umfolozi. It is therefore feasible that capture and removal of a White Rhino could indeed lead to a significant drop in the grazing pressure on a lawn grass area within its vacated home range. In principle, removal of a Rhino is analogous to the situation within the Rhino fence of the ZLGP exclosures. I was therefore able to use Rhino removals as a replicated experiment to test Rhino impacts on the ecology of the grass layer, the grazers, and fire properties relative to controls where no Rhinos had been removed. I had initially planned to use the sink areas as removal treatments and the core area as a control to determine landscape scale effects of Rhino removals. However on closer examination Rhino removals were not

evenly distributed through the sink areas and I decided to focus instead at the level of individual removals.

I wished to define areas of the park to be used as treatments depending on their recent history of White Rhino removal. Removed treatments would correspond to areas from which White Rhino had been recently removed. These areas would then be compared to control treatments in which White Rhino are present. These areas would be analogous with the ZLGP control plots, which are open to grazing by all animal species. Ideally treatment and control areas would be replicated at both the arid (Umfolozi) and mesic (Hluhluwe) ends of the reserve in order to test for the effects of rainfall. If successful this experimental design should prove powerful as it allows for replicated controls and treatments and does not rely on a correlative approach.

In order to select the removed and control areas it was first necessary to map out the distribution of White Rhino and White Rhino removals within the park.

Methods

Definition of Removed Treatments

I obtained data on Rhino removals from the Animal Population Management Database maintained at the Hluhluwe Research Center by the Park Ecologist. This consists of monthly returns provided by the Game Capture unit and also from the various section rangers in the park. These returns give detailed information about many different species within the park. Hence it was first necessary to filter the data in the database so that it only contained information on White Rhino.

The resulting data set ran from the start of 1994 until the 20 of June 2003. Removals occurring after this date are not considered in this thesis. Removals were defined as any event which led to a reduction in White Rhino grazing. This definition allowed me to include events such as mortalities due to poaching, disease or individuals killed by rogue elephants, (Slotow et al. 2000). Seen from the point of the view of the grass layer all of these causes would result in a similar reduction of grazing pressure. The inclusion of these mortalities increased the overall sample size of removals and, also extended the geographic range of the study to the northern end of the park (the majority of Rhino capture operations take place in Umfolozi). I was thus able to study the role of rainfall in altering the effects of White Rhino grazing.

Each record in the resulting dataset contained information on the sex, age and number of Rhino removed as well as the removal date. The location from which the animal(s) were removed was given either by a GPS co-ordinate or referred to a 1 km

square grid covering the park. Since the 1 kilometer grid represented the data with the minimum resolution I used this as the scale at which I mapped Rhino removals. Removals were grouped together by the calendar year in which they occurred and the sum of the number of removals in each grid square per year was calculated.

Data was then transferred into a GIS package (IDRISI, Clark labs) which was used to construct a separate GIS layer for each calendar year in the dataset. Contained in the metadata attached to each GIS layer was a value giving the number of White Rhino removed per grid square per year and this was used to construct a color coded visual scale which represented the 'removal density' (=number of White Rhino removed), in each grid cell. Figure 4.1 illustrates two of the layers that were produced to illustrate removal density.

The data displayed in these map layers was used to help define areas to be used as removed treatments in the landscape scale experiments described in the next two chapters. Removed areas were defined as areas that had gone through a reduction in White Rhino grazing pressure through the removal of White Rhino.

Definition of control treatments

Control areas were defined as areas in which the level of White Rhino grazing pressure had remained unchanged. Ideally the grazing pressure in the control areas should be similar to the grazing pressure that had occurred in the removed areas before the removal took place. In other words controls should be placed in areas occupied by White Rhinos that had not been affected by removals: not in areas from which White Rhinos

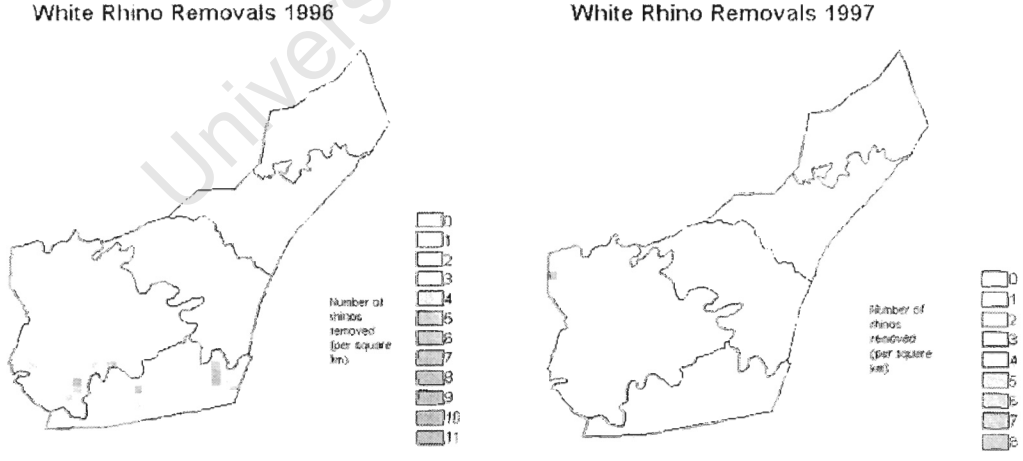


Figure 4.1. Examples of GIS layers showing the spatial arrangement of White Rhino removals in (a) 1996 and (b) 1997. Number of removal per grid square ('Removal density') is given by the scale on the right of each map.

had not been removed because there were none there to remove in the first place. In order to define control areas I needed to have some idea of the spatial distribution of White Rhino in the park.

This data comes from two sources: firstly the annual aerial sink counts and secondly the biennial game transects. Sink counts give a better idea of the spatial distribution of White Rhino but unfortunately they are only flown over Umfolozi and do not include data for Hluhluwe. Hence when defining control areas I used data from the sink counts in Umfolozi (where the majority of removals occur) and data from the game census in Hluhluwe.

Data on the numbers and positions of White Rhino were extracted from this data set and plotted on a 1km grid system in a similar fashion to the removal data above. Again GIS layers were developed for each year of data from 1994 to 2002. Examples of these layers are shown in figure 4.2.

Data from the biennial game census has been digitized and entered into GIS layers, but due to its nature it is not possible to display the data on the grid system used for the rest of the data. Instead it is only possible when identifying study sites to examine the nearest transect for records of White Rhino sightings in the vicinity.

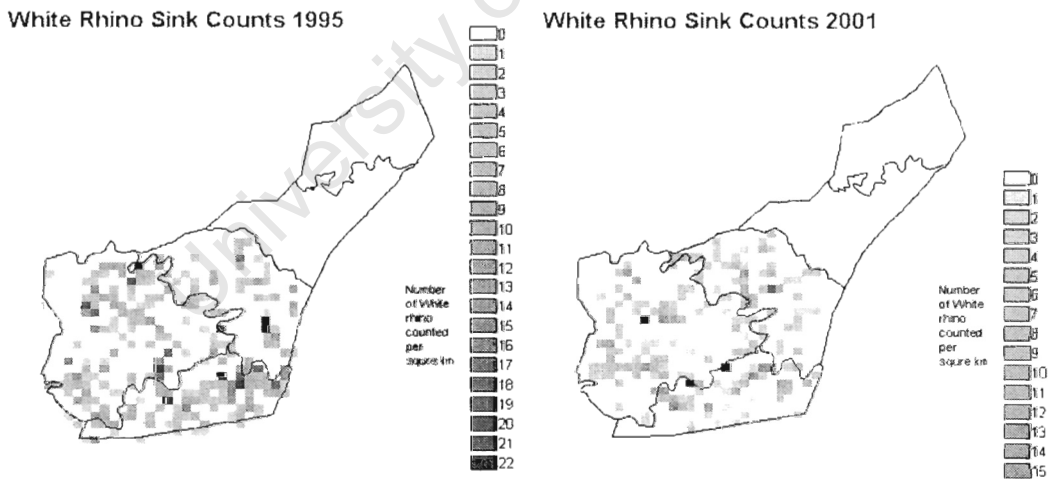


Figure 4.2 Examples of GIS layers showing the spatial distribution of White Rhino sightings based on annual sink counts flown in a fixed wing aircraft for a) 1995 and b) 2001. Data is presented in a 1 km square grid with the number of White Rhino observed in each grid square indicated by the legend on the right. Note that data only covers the Umfolozi section of the reserve, as flights do not occur over Hluhluwe.

Limitations of data and caveats

There are several possible problems with the treatment of data and assumptions made in this chapter. One possible source of error in the database of Rhino removals is that the positions recorded by the game capture team refer to the point at which the animal was picked up by the ground team and loaded into its transportation crate. In some cases it may be necessary to use the helicopter to herd the animal to a location more easily accessible by the ground crew before darting and capturing it. If this were the case and the animal was chased outside of its home range then the information in the database would not refer to the area where the reduction of grazing pressure had occurred. However, in most instances of game capture it is not necessary to pursue animals far from the area where they are originally sighted (V. van Heerden, game capture helicopter pilot, pers. comm.)

Another likely confounding factor would be the rapid recolonising movement of White Rhinos from outside grid squares into squares designated as treatments. This would have the effect of replacing the grazing pressure which departed along with the originally removed Rhino reducing any difference between control and removed areas. However despite an area being classified as 'removed' it is still likely to contain some Rhinos. Owen Smith found that in Umfolozi White Rhino females have overlapping home ranges that are shared by a number of other females and their offspring. Males have much smaller territories which they will defend against any other dominant bulls. However they will tolerate younger subordinate bulls and females with calves in their territory (Owen-Smith 1975). Hence even in a case where multiple Rhinos have been removed simultaneously from a grid square it is likely that there will still be some resident Rhinos in that area. For this reason the removed area would not be as attractive to animals from outside the removed grid square as they would be if they had been completely emptied of all Rhino.

Secondly the changes that have occurred to the grass layer within the ZLGP fences have often occurred quite rapidly (chapter 3) and it is hoped that these changes would occur before any recolonisation had occurred.

The data on White Rhino distribution obtained from the sink counts also has a number of potential problems. Firstly data from the sink counts can only be regarded as a snapshot of the distribution of White Rhino in the park at the moment that the census was flown, which is usually in the late dry season (Oct/Nov). White Rhino do show seasonal

movements, often going in search of water and better grazing during dry periods (Owen-Smith 1988), although they show fidelity to home ranges to which they will usually return. These movements may result in differences in distribution of White Rhino between the time the surveys were performed in the late dry season and the time when fieldwork was done.

For the reasons listed above, the 'removal' treatment in this landscape experiment is less extreme than the Rhino exclosures described in the previous chapter and is likely to vary more among 'replicates'.

Compilation of spatial database

All the data that was formatted to the 1km grid system was compiled into a single 'group file' which contains, in its associated metadata, all values for Rhino counts and Rhino removals for all years between 1994 and 2003. This spatial database (Fig 4.3) gives one the ability to select onscreen a particular grid cell and then have its entire history of removals and number of Rhino counted during sink counts displayed as far back as 1994. Further GIS layers such as roads or contours can then be added in order to help in the recognition of specific areas on the ground. Alternatively points can be marked and then downloaded onto a handheld GPS unit to help identify areas in the field. It is also possible to overlay aerial photos to aid in the identification of different habitat types or features such as wallows (see chapter 5).

This database could then be interactively queried and used to select areas within the park to be used as both treatments and controls.

Results

During the period January 1994 to March 2003 a total of 1108 White Rhinos were removed from the park with the vast majority of these (960) coming from Umfolozi. Taking the weight of an adult White Rhino as two metric tones (Owen-Smith 1988, Kingdon 1997) this represents the removal of a total of 221 tones of grazing biomass per annum. A detailed breakdown of these numbers is given in figure 4.4.

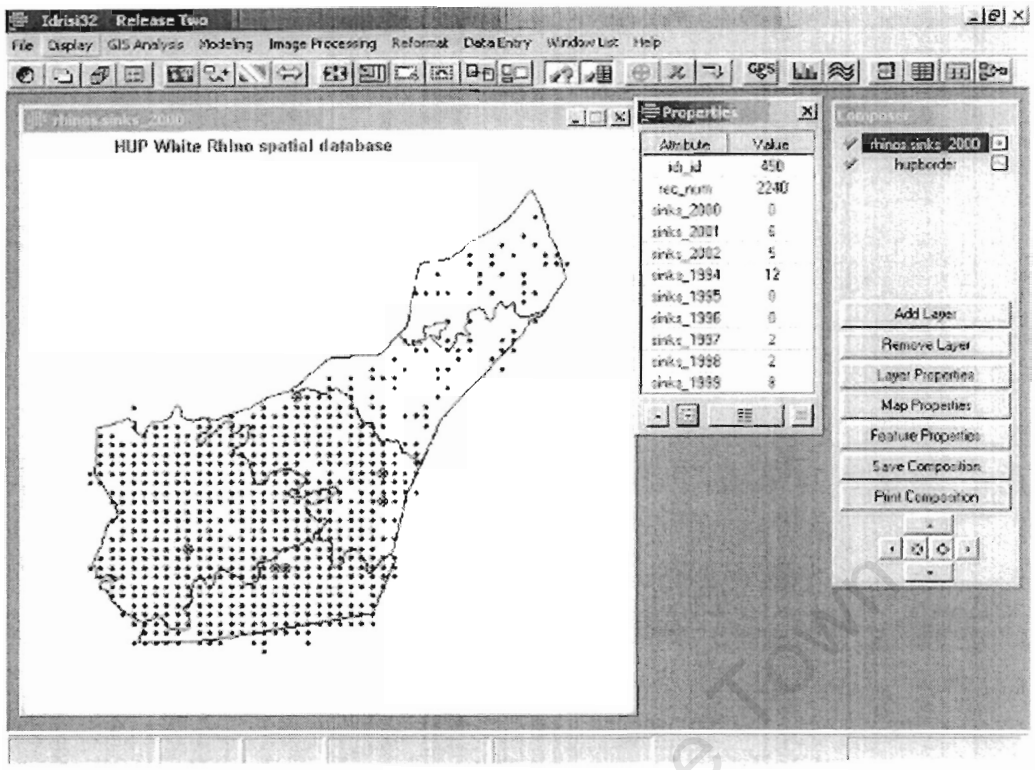


Figure 4.3. The spatial database of White Rhino removal and distribution data. Points could be selected with the mouse in the map window (left) and the information about Rhino removals and counts is displayed in the properties window (center).

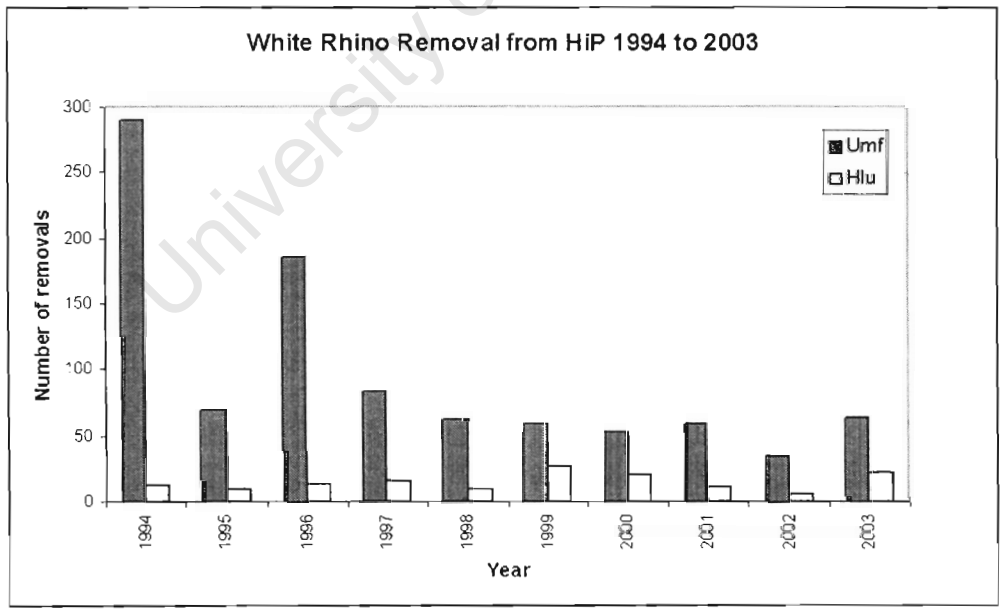


Figure 4.4

Total numbers of White Rhino removed from Hluhluwe and Umfolozi per year for the years 1994 to 2003.

Discussion

I was successfully able to create GIS layers giving surfaces of rhino density and removals for the years 1994 to 2003. I will use these layers in subsequent chapters in order to define control areas (non-removed areas with White Rhino present in them) and removed treatments (which have undergone a reduction in the number of White Rhino). These areas will then be used to test the hypothesis that emerged from chapter 3 at a landscape scale. However the layers are subject to the inaccuracies already noted in this chapter (see 'Limitations of data and caveats', above) and these should be borne in mind when discussing results in later chapters that are based on experimental designs using the GIS layers generated in this chapter.

5 Measurement of grass around wallows. Are White Rhinos acting as keystone species?

Introduction

In this chapter I explore the role of White Rhino in structuring the savanna ecosystem in HiP at a landscape scale. Results of the exclosure experiments reported in Chapter 3 suggest that White Rhino are the main agents controlling grass height at the wetter end of the park where grass growth is more vigorous. In doing so they are creating lawns that are utilised by other species of grazers which prefer to feed on short grass such as Impala, Zebra and Wildebeest. As such they would be acting as keystone species in the system. When they are removed lawn grass areas would be lost as the standing grass biomass increases. Conversely, the exclosure results at the arid end of the park suggest that species other than White Rhino are capable of maintaining a short grass sward and that Rhino have less of an ability to shape the landscape. This leads to the expected results of Rhino presence or absence illustrated in figure 5.0.

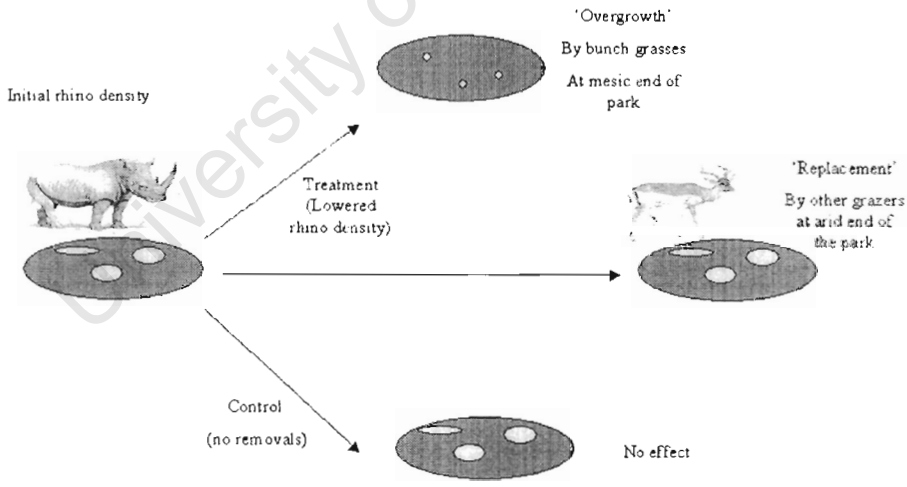


Figure 5.0. The proposed role of White Rhino in structuring savannas and possible consequence of their removal. Darker areas represent bunch grasslands and lighter patches represent grazing lawns.

In order to investigate this hypothesis I needed to take measurements of the grass species and height and to quantify the numbers of other species of grazing animals using areas assigned to the two different treatments defined in chapter 4. The treatments would either be an area from which White Rhino were removed during 2003 (termed the removal area), or an area in which White Rhino are present and had not been removed (termed the control area). However measuring all the grass in the 1km grid cells used to define treatments proved to be a daunting prospect. It soon became apparent during trials of my field method that I needed points within each of the 1km grid squares at which I could focus my sampling efforts.

Wallows are depressions in ground in which water collects during the rainy season. They are used by some grazers for ectoparasite control and thermoregulation during the summer. Wallows are self constructed by the animals which use them, particularly Buffalo, White and Black Rhino and Warthogs and they may persist as artifacts in the environment for long time periods (Knapp et al. 1999) providing an ecological inheritance to future generations of the species that created them. This process has been termed 'niche construction' (Day et al. 2003, Laland and Odling-Smee 2003) Wallows are a conspicuous feature of habitats containing natural assemblages of herbivores in Africa. They provide habitats for species adapted to ephemeral pools, have been shown to influence patch dynamics (Uno 1989), and are often congregating points for animals. They are usually surrounded by highly grazed areas of grasses, often forming grazing lawns. This in turn attracts animals that do not indulge in wallowing behavior such as Zebra, Impala and Wildebeest. I propose that any localized drop in grazing pressure caused by White Rhino removals would be evident in the lawns surrounding wallows. Hence I used wallows as focal points within my 1km study areas, around which I would conduct my sampling.

I located wallows from a set of aerial photos of the park taken in 1997. These photos had been scanned into digital format and georeferenced. I opened these images in a GIS program. Large wallows were visible on these photos as darker areas, usually with a characteristic pattern of radiating game paths which stood out as lighter traces (figure 5.1). Wallows were marked with points in the GIS program and these points were downloaded into a handheld GPS unit which assisted in locating wallows in the field. Other wallows were identified from my own experiences walking in the park and by talking to rangers and other researchers. Thirdly a number of reconnaissance walks were conducted in potential study areas and the positions of wallows recorded on a handheld

GPS device. After locating wallows, I used the spatial database developed in chapter 4 to assign them to either the control or the removed treatments.

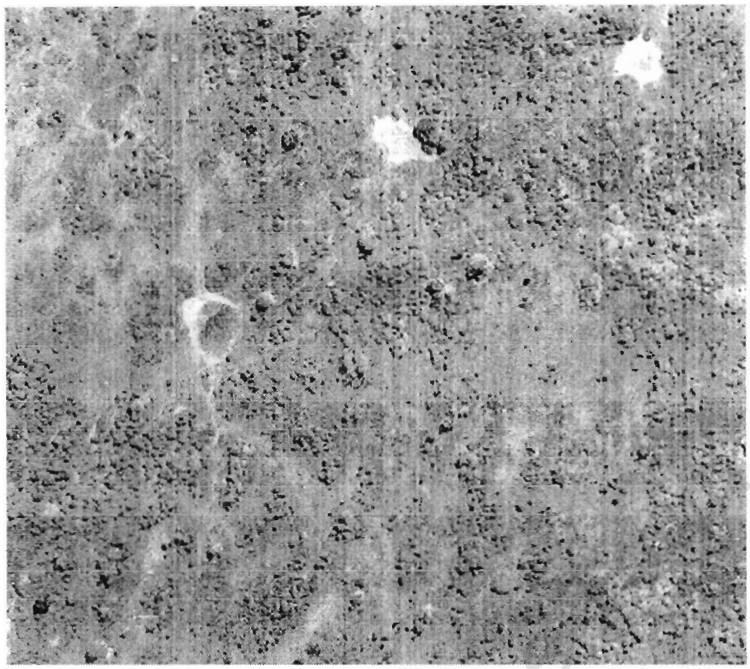


Figure 5.1. Wallows as identified from aerial photography.

Methods

I sampled the grass around the wallows on three occasions through 2003-2004 in order to follow changes in grass height through an entire growing season. In order to do this I divided the growing season into three sample sessions and took measures of the grass around the wallows during each session. Dates of sample sessions and the number of wallows sampled are given in table 5.1.

Table 5.1

The dates over which sampling was conducted and number of wallows sampled (#). (Note that T1 was my initial field trial, data from which is not included in this analysis.)

Sample Period	Hluhluwe	#	Umfolozi	#
T2	27/08/2003 > 03/09/2003	19	N/A	
T3	07/01/2004 > 12/01/2004	21	13/01/2004 > 16/01/2004	30
T4	04/05/2004 > 06/05/2004	21	10/05/2004 > 13/05/2004	31

Unfortunately it was not possible to perform the first sample session in Umfolozi and as a result only two sets of samples were taken at the arid end of the park. The slight differences in sample sizes can be accounted for by the fact that some wallow surveys had to be abandoned due to a large herd of elephants.

I sampled eight transects around each wallow as illustrated in figure 5.2. The first transect (transect 1) began at the northernmost edge of the wallow and was walked on a compass bearing due north. Transects were 60m long and began at the point at which the grass layer surrounding the wallow became continuous. Once a transect had been completed I returned to the edge of the wallow and conducted the next transect in a north easterly direction, in other words 45 degrees clockwise from the original transect. This process was repeated until a total of eight transects had been measured, each radiating out from the wallow in a different direction. Although every effort was made to stick to this protocol it was sometimes necessary to arrange transects in such a way that they did not pass through areas of dense bush.

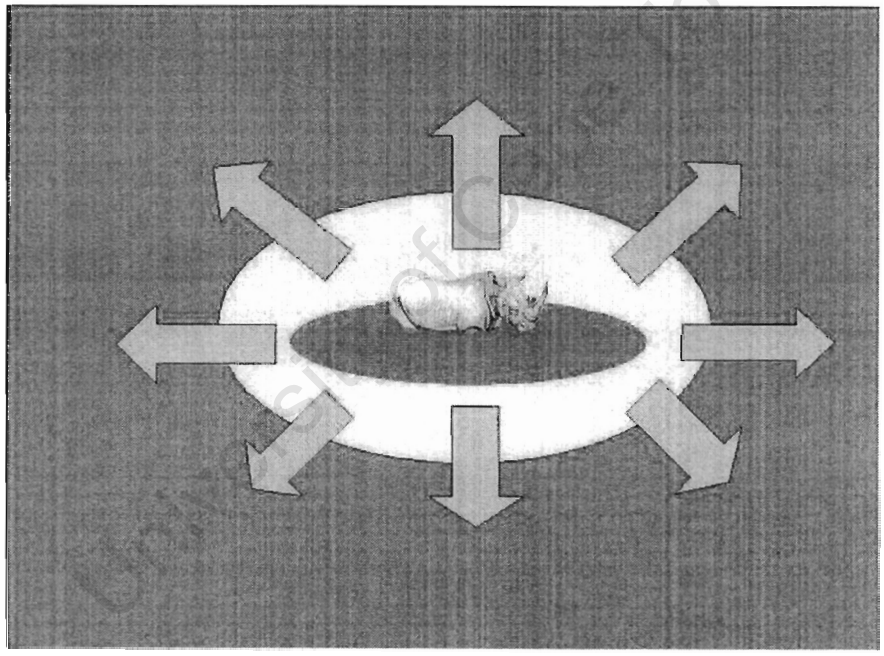


Figure 5.2. Showing arrangement of transects around a wallow. Grass height and species composition and the occurrence of animal dung was measured along each transect.

Measurement of grass height and species

Readings of grass height were taken with a Disc Pasture Meter (DPM) (Bransby and Tainton 1977). When taking DPM measurements care was taken to avoid woody plants hidden within the grass layer which might give erroneous readings. DPM measurements were taken every 5 meters along the transect until 12 readings had been

obtained. Whilst recording grass height the three most dominant species of grass occurring under the disc were also recorded.

Data analysis of the grass height data began with visual interpretation of Box plots. The response variable used in constructing these graphs was the median DPM reading per transect. I preferred to use the median instead of the mean as it is less affected by outlying data points. As a preliminary analysis I drew graphs of grass height around wallows in Hluhluwe and Umfolozi and subsequently separated this data into removed and control groups. Differences between groups were analysed using oneway ANOVAs. Data was tested for unequal variances with Levene's, O'Brien's and the Brown-Forsythe tests. Data found to have unequal variances around the mean were instead analysed with a Welch ANOVA which account for skewed variance. However it is assumed in the above analysis that transects around wallows were independent of each other. This is unlikely to be true as transects are not independently spatially located but grouped together around wallows. This could lead to the assumptions of the statistical test being violated and hence give a false result, particularly if the transects showed significant autocorrelation. In acknowledgment of this, I also calculated the amount of short grass around each wallow by counting the number of DPM readings less than or equal to 5 cm. I plotted these DPM values (as the response variable) for both control and treatment wallows at both ends of the park. This data was then analysed with a Wilcoxon test. The variances of the data were tested for homogeneity using a combination of O'Brien, Brown-Forsythe, Levene and the Bartlett test for unequal variance.

In order to formally test whether the removal of White Rhino accounted for the difference in grass height around wallows or whether other factors could also account for the variation I constructed a general linear model (GLM). I tested to what extent the grass height (the response variable, DPM at sample time t4) could be predicted by the other variables that were entered into the model. These predictor variables were:

transect distance - the distance along each transect that the DPM was taken.

treatment – Whether a wallows was in a treatment (1) or control (0) area

park - Hluhluwe or Umfolozi.

elevation - of the wallow (meters above sea level). This was obtained from the GPS co-ordinates of the wallows and a GIS coverage giving altitude and is correlated with rainfall (Balfour and Howison 2001). Unfortunately it was not possible to measure actual rainfall at each of the wallows.

I initially entered all these variables into the model and crossed them to examine any interactive effects. I then selected the variables explaining the most variation for a final or reduced model.

I tested for treatment effects on grass species composition by recording species under the disc at each DPM. Grasses that were ranked as the first or second most dominant species were given a score of 2. Grasses ranked as the third most dominant species received a score of 1. (This was because in my experience there is little difference in the amount of ground covered by either of the first two most dominant species). The scores for each grass were summed for each wallow at time T4. The distribution of scores for wallows in both treatments and controls in Hluhluwe and Umfolozi were examined separately for each grass species. I also looked at the difference between species scores for each wallow between samples 3 and 4 (January to May 2004) and tested for statistically significant changes using a one-way ANOVA.

Measurement of animal usage

I estimated the number of other grazers utilizing the grass around each wallow by recording the presence or absence of dung in the 5 meters between each DPM measurement. Only fresh dung was counted. (Dung was judged as fresh if it had not begun to decompose, i.e. did not crumble easily in the hand or had been attacked by termites). I calculated the total amount of dung around each wallow for each animal species by summing the presence/absence scores for each species. In order to test for differences in the amount of dung around control and treatment plots I used an oneway ANOVA test. I first tested for homogeneity of variance using a combination of Levene's, O'Brien's and the Brown-Forsythe test. I then tested for significant differences between groups with a *post hoc* Wilcoxon test.

Results

The summer of 2003/4 was a very dry period with drought conditions across much of Northern Kwa-Zulu. Significant rains only fell in the latter part of January (when 150mm fell on the 23rd alone). The pattern of rainfall during this period is illustrated in figure 5.3, where it is compared to the average values from the previous twenty years. This effectively meant that my first two samples sessions were taken during an extended dry season and only the last session of data collection occurred after the onset of major rains when plants were actively growing. Another anomaly was that during this period Umfolozi received more rainfall than Hluhluwe did.

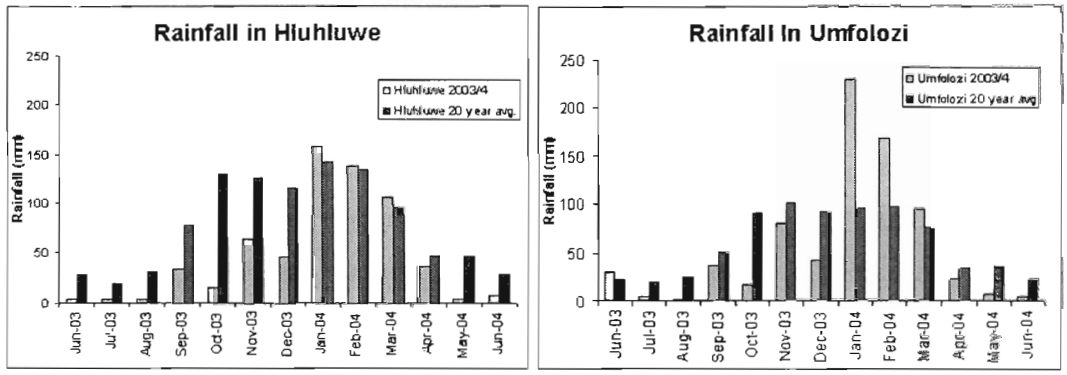


Figure 5.3. Monthly rainfall during 2003/4 growing season compared to the 20 year average for a) Hluhluwe and b) Umfolozi. (Rainfall data comes from the ZLGP data and KZN Wildlife long term records.)

Variation in grass height

During the course of the three sampling periods I sampled 53 wallows 122 times taking a total of 11,721 DPM/species composition readings. Figure 5.4 illustrates the change in grass height (DPM in cm) over the course of the study period at both ends of the park. The effect of the rainy season, which started between sample sessions 3 and 4, is obvious.

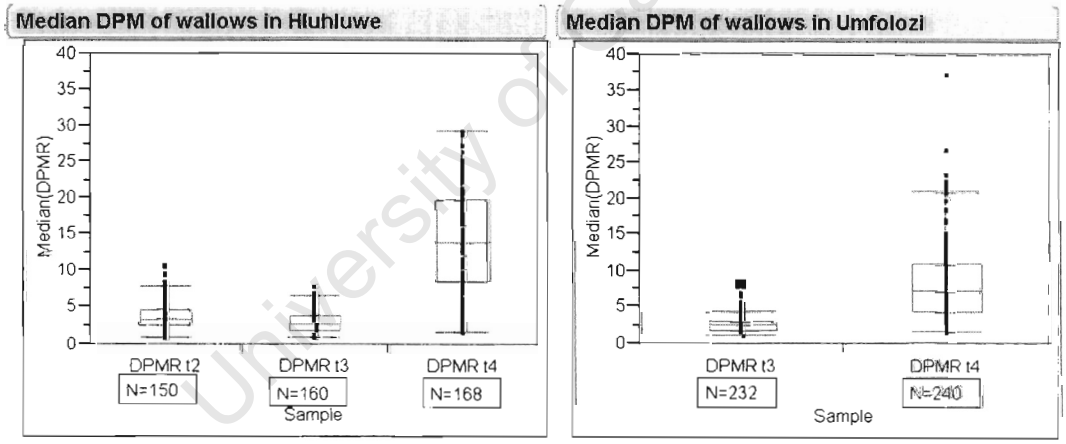


Figure 5.4. The grass height (cm) as measured with a DPM around wallows in Hluhluwe and Umfolozi through the 2003/4 growing season. t2 = Aug/Sept 2003, t3 = Jan, t4 = May 2004. The median DPM for each transect was taken. Sample size (N) = number of transects (eight per wallow). Boxes represent 25% and 75% quartiles, the middle line represents the mean and the whiskers represent 90% percentiles.

Figure 5.5 separates the data used in Figure 5.4 into the two treatments giving a total of four graphs. In Umfolozi both the control and removal treatments showed an increase in the grass height towards the end of the season but this increase was similar around both control and removed wallows (6.45 cm mean increase in DPM around

removed areas as opposed to 5.00 cm mean increase in DPM around control wallows). In Hluhluwe the increase in grass height towards the end of the growing season was greater than Umfolozi around both treatments. The largest increase was around wallows in areas from which White Rhino had been removed (12.93 cm DPM mean increase in removal areas as opposed to 9.9 cm DPM mean increase around controls).

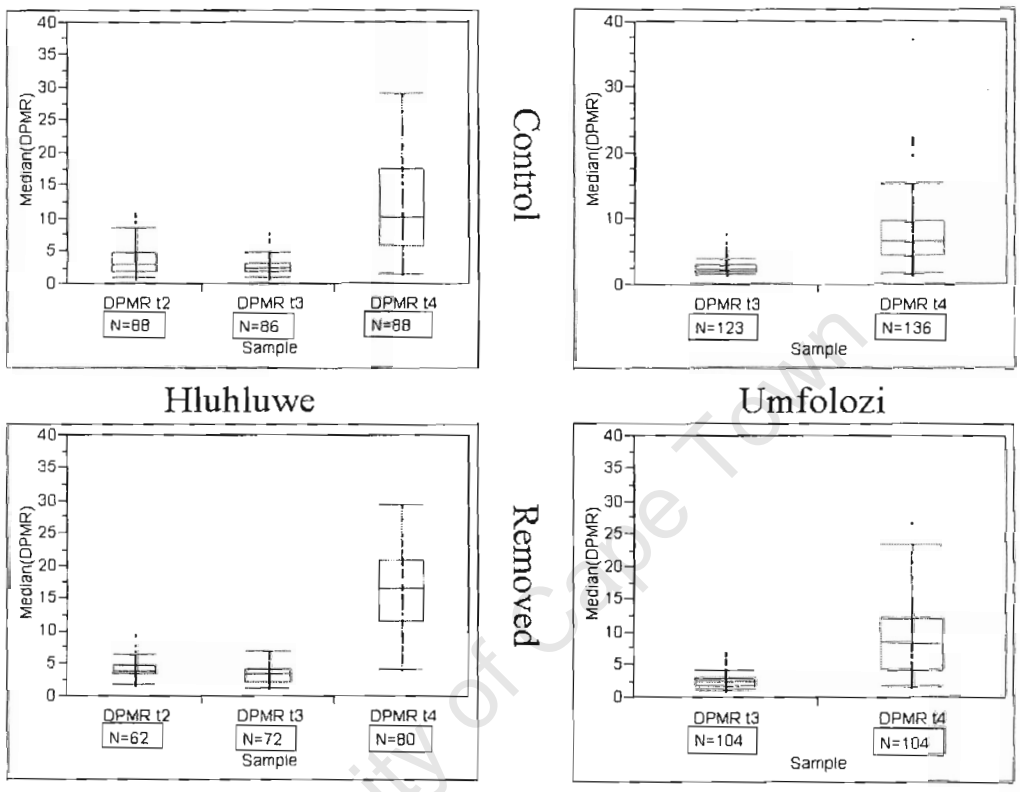


Figure 5.5. Median DPM (cm) around Rhino removal and control wallows in Hluhluwe and Umfolozi. N= sample size (number of transects).

Figure 5.6 shows grass height around both control and removal wallows in Hluhluwe and Umfolozi using only data from sample time t4 (a sample size of 5100 DPM readings) when the late rains had stimulated grass growth. In Hluhluwe, there was a greater increase in grass height around removal wallows than around control wallows. This seems to indicate that there is some release effect on the grass in Hluhluwe when White Rhinos are removed. The effect of Rhino removal around wallows in Umfolozi was much smaller. The results of a oneway ANOVA are given in table 5.2. This confirmed that at the end of the growing season there was significantly more grass around removed wallows in Hluhluwe compared to controls. The grass around removed wallows

in Umfolozi was also significantly taller than that around control wallows although at a much lower level of significance.

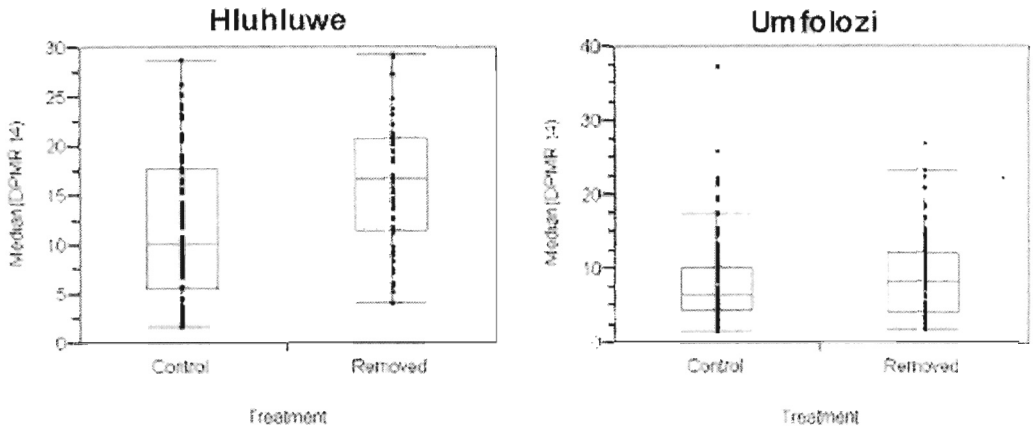


Figure 5.6. Grass height (cm), measured with a DPM, around control and removed wallows in Hluhluwe and Umfolozi at sample time T4 (May 2004). Boxes represent 25 and 75 % quantiles and center lines indicate means.

Table 5.2. Mean DPM values (cm) at sample time t4 with standard error (SE) and the results of a *post hoc* Wilcoxon test on the data in figure 5.6. Df's = degrees of freedom, Z= test statistic and Prob>Z= chance of test statistic occurring through chance alone.

	control		removed		Wilcoxon test		
Park	MeanDPM	SE	Mean DPM	SE	df's	Z	Prob>Z
Hlu	16.4	0.7	11.9	0.7	166.0	4.1	<0.0001
Umf	9.1	0.5	7.6	0.4	238.0	1.7	<0.0873

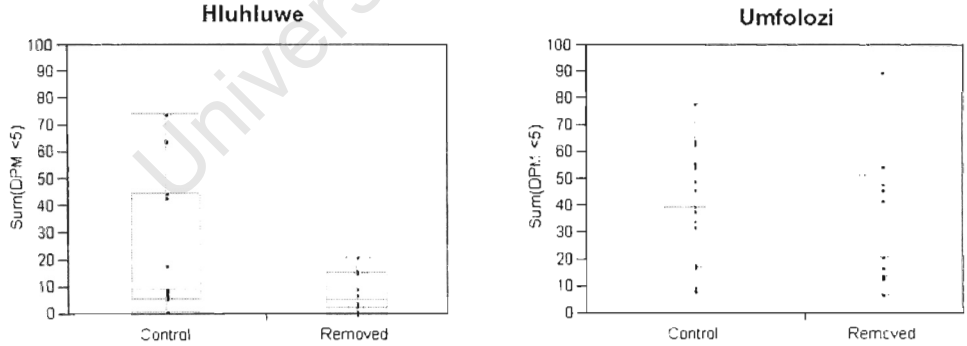


Figure 5.7. The amount of short grass (DPM <=5 cm) around control and removal wallows at both ends of the park.

Table 5.3. Results of Wilcoxon tests of the amount of short grass (DPM<5cm) around wallows.

Park	Treatment	N	Mean	SE	Lower 90%	Upper 90%	Prob>Z
Hlu	Control	11	25.1	6.0	12.5	37.7	0.0623
	Removed	10	7.9	6.3	-5.3	21.1	
Umf	Control	18	39.4	7.7	23.6	55.3	0.8769
	Removed	13	41.5	9.1	22.9	60.2	

Figure 5.7 shows the amount of short grass (defined as DPM readings less than or equal to 5cm), around each wallow. It is evident that there is a lot of variance in the extent of grazing patches around wallows. Biologically this equates to heterogeneity or patchiness among different wallows. Removal of Rhino in Hluhluwe led to less short grass and reduced variance in the data, i.e. the grass was taller and more uniform. Table 5.3 gives the results of the analysis of this data. Data from Hluhluwe had higher a variance (F test, $P < 0.05$) and data from Umfolozi equal variances, indicating that Rhino removals significantly reduced variability among wallows in Hluhluwe but not in Umfolozi.

The results from general linear model analysis are given in table 5.5. With all of the variables entered into the model and crossed, the model predicted a quarter of the variation in grass height ($R^2 = 0.25$) The predictor variables that explained the greatest amount of variation in DPM (according to the sums of squares) were **park** followed by **elevation** and then **transect distance**. **Treatment** explained the least amount of variation in the DPM reading. The effect of all these variables was significant at the 0.001 level. The predictor variables were crossed against each other in order to examine any interactive effects that might exist between them. The only combination which had a greater sums of squares than the values for the separate predictors was the cross park*elevation ($P < 0.001$). Although treatment * elevation was also significant it was not included in the final model due to its low sums of square values.

Hence in my final selection of parameters for the reduced model I chose the four individual and one combined parameter (table 5.5, $R^2 = 0.25$).

In order to test that the assumptions behind the model were correct I plotted a distribution of the residual values (the difference between observed and predicted values) against the observed values and found little evidence in the distribution of points for any unexplained trends. I also plotted the residual values against all the predictor variables together with variables that were not include in the original model, such as the removal density in any given year but again found no relationships indicating that they improved

accuracy of the model. I also checked that the predictor variables were not co-correlated. There was significant correlation between the term park and elevation. However as Hluhluwe is on average higher than Umfolozi this could not be avoided.

Variation in grass species composition

I could find no significant differences indicating shifts in grass species composition either between removed and control wallows (table 5.4) or differences in the way the summed scores changed through time (from January to May).

Table 5.4 Analysis of grass species scores at control and removed wallows for the last sample period (T4). Data for the 7 most numerous species of grass is given. N=sample size, SE=Standard error, Prob>Z = chance of test statistic occurring through chance alone.

Grass species	Park	Treatment	N	Mean	SE	Upper 90%	Lower 90%	Prob>Z
Bothriochloa insculpta	Hlu	Control	11	39.82	8.45	22.06	57.58	0.2701
		Removed	9	18.22	9.34	-1.41	37.85	
	Umf	Control	17	36.76	7.33	21.72	51.81	0.9293
		Removed	12	30.67	8.73	12.76	48.57	
Chloris virgata	Hlu	Control	11	17.36	6.78	3.12	31.61	0.1091
		Removed	9	30	7.49	14.26	45.74	
	Umf	Control	17	16.18	5.88	4.12	28.24	0.6188
		Removed	12	24.17	7	9.81	38.52	
Digitaria longiflora	Hlu	Control	11	10.09	4.51	0.63	19.56	0.1258
		Removed	9	15.78	4.98	5.31	26.24	
	Umf	Control	17	26.65	12.19	1.64	51.65	0.2589
		Removed	12	48.5	14.51	18.74	78.26	
Panicum maximum	Hlu	Control	11	44.27	10.08	23.1	65.45	0.4464
		Removed	9	19.89	11.14	-3.52	43.3	
	Umf	Control	17	39.06	7.82	23.01	55.1	0.9647
		Removed	12	31.5	9.31	12.4	50.6	
Sporobolus pyramidalis	Hlu	Control	11	50.73	15.44	18.28	83.17	0.101
		Removed	9	86.78	17.07	50.91	122.64	
	Umf	Control	17	50.06	13.99	21.35	78.77	0.6512
		Removed	12	60.17	16.65	25.99	94.34	
Themeda triandra	Hlu	Control	11	49.55	12.85	22.55	76.54	0.9697
		Removed	9	35.78	14.2	5.94	65.62	
	Umf	Control	17	42.29	9.86	22.06	62.53	0.1263
		Removed	12	61.58	11.74	37.5	85.67	
Urochloa mosambicensis	Hlu	Control	11	37.36	17.1	1.44	73.28	0.7535
		Removed	9	35.11	18.9	-4.6	74.82	
	Umf	Control	17	49.06	18.12	11.88	86.24	0.2903
		Removed	12	22.75	21.57	-21.51	67.01	

Table 5.5. Model parameters of the General linear model built to predict grass biomass around wallows. Both the full and reduced model are given. Variables marked in bold were included in the final model. Probabilities marked in bold are significant at the <0.001 level. Estimate gives size and direction of effect, SE=standard error of predictor variable, df=degrees of freedom, f ratio= computed test statistic, prob>f= chance of statistic being exceeded by chance alone. The value sums of squares indicates the amount of variation in the data set explained by each variable.

Variable	estimate	SE	df	f ratio	prob>f	sum of squares
Full model (R-square=0.258)						
Intercept	-1.917	0.743				
transect dist	0.506	0.033	1	231.417	**<0.001**	14615
treat of Wallow.02[0]	-0.965	0.12	1	65.035	**<0.001**	4107
(transect dist-6.5)*treat of Wallow.02[0]	0.022	0.034	1	0.399	0.528	25
park[h]	2.846	0.116	1	605.436	**<0.001**	38236
(transect dist-6.5)*park[h]	0.015	0.033	1	0.212	0.645	13
treat of Wallow.02[0]*park[h]	-0.182	0.122	1	2.24	0.135	141
ELEVATION	0.055	0.004	1	232.208	**<0.001**	14665
(transect dist-6.5)*(ELEVATION-191.223)	-0.001	0.001	1	0.824	0.364	52
treat of Wallow.02[0]*(ELEVATION-191.223)	0.014	0.003	1	19.817	**<0.001**	1251
park[h]*(ELEVATION-191.223)	0.077	0.004	1	396.642	**<0.001**	25049
Minimal model (R-square=0.254)						
Intercept	-2.319	0.736				
Park [h]	2.883	0.115	1	627.25	**<0.001**	39748
Transect distance	0.504	0.036	1	239.356	**<0.001**	15167
Elevation	0.056	0.004	1	244.951	**<0.001**	15522
Treatment [0]	-0.946	0.118	1	61.128	**<0.001**	4063
Park*Elevation	0.085	0.004	1	598.434	**<0.001**	37922

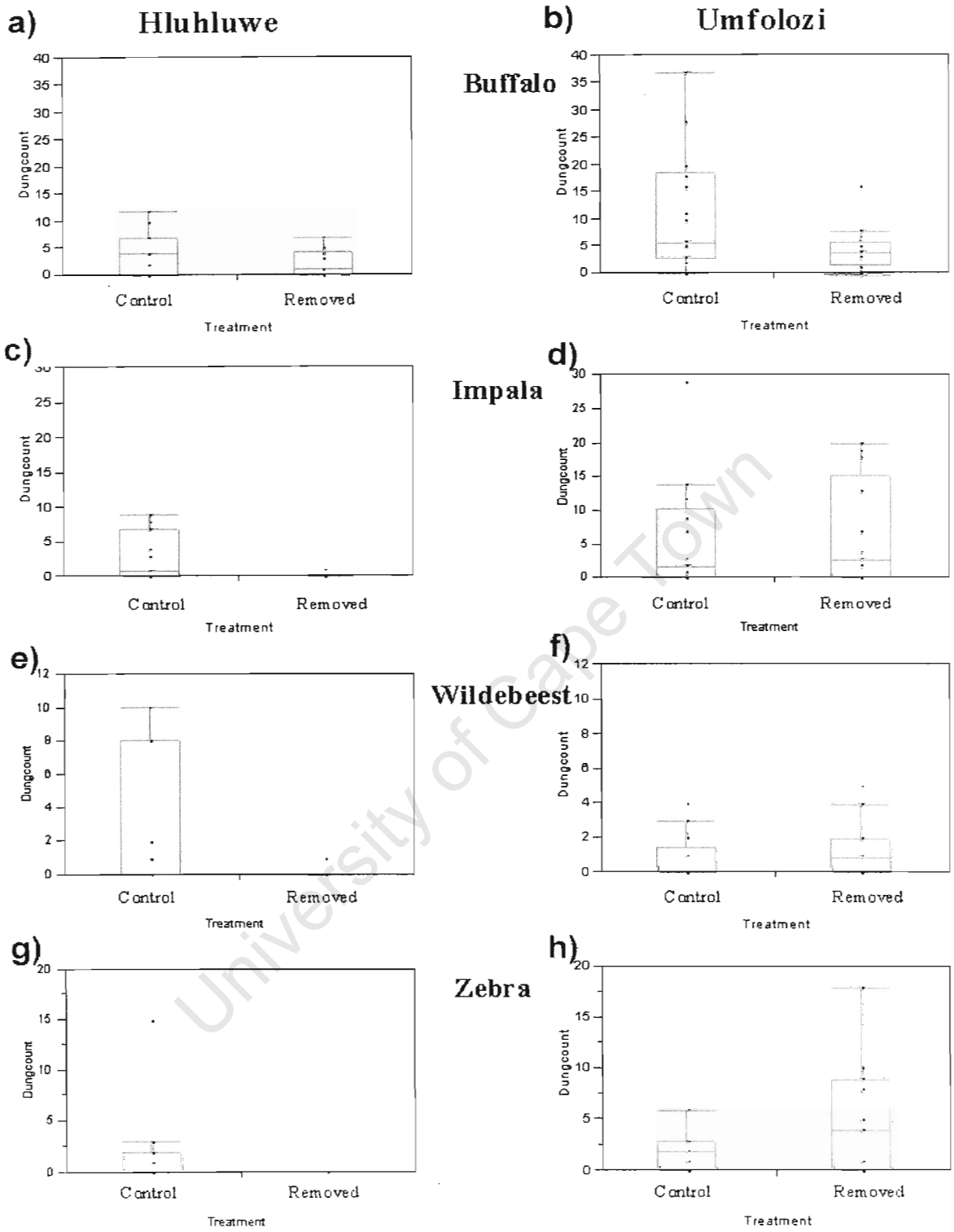


Fig. 5.8. The number of dung piles of grazing species counted around wallows of both treatments: a) Buffalo dung in Hluhluwe, b) Buffalo dung in Umfolozi, c) Impala dung in Hluhluwe, d) Impala dung in Umfolozi, e) Wildebeest dung in Hluhluwe, f) Wildebeest dung in Umfolozi, g) Zebra dung in Hluhluwe, h) Zebra dung in Umfolozi. Data from all sampling periods is included. Boxes give 25 and 75% quantiles, whiskers 90% quantile and the center line gives the mean

Variation in Dung count data

I counted 2,135 separate pieces of dung or dung piles belonging to 14 different animal species during my three sample periods. I calculated the total amount of dung per species per wallow for the most common species (figure 5.8) with wallows separated by park and grouped to treatment. The general pattern in Hluhluwe was that there was less dung from grazers in areas from which Rhino had been removed compared to control areas. This was true for all species though significant (at P> 0.05) in only impala and zebra. In Umfolozi there were no significant differences between the amount of dung around control and removed wallows. Statistical results are given in Table 5.6.

Park	Grazer	Treatment	N	Mean	SE	Lower 90%	Upper 90%	Prob>Z
Hluhluwe	Buffalo	Control	11	4.8	1.1	2.6	7.0	0.15
		Removal	10	2.1	1.1	-0.2	4.4	
	Impala	Control	11	2.9	0.8	1.3	4.6	0.03
		Removal	10	0.1	0.8	-1.6	1.8	
	Wildebeest	Control	11	2.6	0.9	0.8	4.5	0.06
		Removal	10	0.1	0.9	-1.8	2.0	
	Zebra	Control	11	2.0	1.0	0.0	4.0	0.02
		Removal	10	0.0	1.0	-2.1	2.1	
Umfolozi	Buffalo	Control	17	11.5	2.2	7.1	16.0	0.11
		Removal	13	4.5	2.5	-0.6	9.5	
	Impala	Control	17	5.8	1.9	1.9	9.7	0.97
		Removal	13	6.6	2.2	2.2	11.1	
	Wildebeest	Control	17	0.9	0.4	0.1	1.7	0.37
		Removal	13	1.3	0.4	0.4	2.2	
	Zebra	Control	17	2.1	1.0	0.1	4.0	0.21
		Removal	13	5.0	1.1	2.8	7.2	

Table 5.6. Results from Oneway ANOVA and a *post hoc* Wilcoxon test. N=sample size, SE=standard error, Prob>Z=probability of test statistic (Z) being met through chance alone.

Discussion

I will discuss results for dungcounts, grass height and species separately, before moving to a more general discussion of the results.

Grass Height

As grass height increased during the growing season there was a significant difference in the grass height around control and removed wallows, with a larger effect in Hluhluwe than in Umfolozi. Grass height around wallows was heterogeneous (patchy) especially in Hluhluwe. Removal of Rhinos led to a decrease in this patchiness in Hluhluwe. Simple analysis of variance showed significant differences in

grass height between removed and control wallows, particularly in Hluhluwe. Analysis of the amount of short grass also showed a treatment effect in Hluhluwe, though this was not quite significant at the 0.05 level of probability. The general linear model indicated that several factors had an influence on grass height including the removal of White Rhino. The model predicted a relatively low percentage of the variation in the data (25%) indicating that a lot of the variation in the grass height data was unaccounted for. This points to the presence of random noise in the data set or at least variation that is accounted for by variables that I did not include in the model, such as soil type. However there was a highly significant effect of Rhino removal on grass height accounting for just under 2 cm of the variation in DPM reading. In contrast knowing which end of the park you were in could identify almost 6cm of the variation in grass height. This effect of Rhino removal could be viewed as a negligible amount of variation with little biological importance. On the other hand it can be thought of as impressive that amidst all the variability found in the savanna ecosystem I have managed to predict even this small effect from only a knowledge of recent rhino removal history. Even relatively small changes in grass height can radically alter the properties of an ecosystem (see chapter 3).

Dungcounts

The dungcount data is a surrogate for the amount of grazing by other species of animals, assuming that there is a linear relationship between the amount of dung around a wallow and the amount of grazing by a particular species. This assumption may not be wholly valid as dung deposition is not homogenous in either space or time or between species. For instance some species deposit dung preferentially in dung piles or middens. Barnes gave a review of the efficacy of using dungcounts to estimate and detect change in population numbers (Barnes 2001). He found that dungcounts were as good as any other method for the estimation of animal numbers. Here I used dung not as an estimate of actual animal numbers but only as an index of animal utilisation of an area and how this has changed through time (i.e. between sample sessions and within species). Other methods for estimating the numbers and species of grazers include spoorplots and video cameras. However spoorplots suffer from similar problems to dungcounts in that they do not necessarily indicate that an animal has fed in an area. They are also laborious in both implementation and

maintenance and not suited to a study such a mine. Thus as a quick and non-destructive measure of grazing pressure, dung counts are unrivalled.

The general pattern seen in the graphs in Figure 5.8 was one of decreasing numbers of grazers around the removed wallows in Hluhluwe. In Umfolozi there was no significant treatment effect although it appeared from figure 5.8 that there was slightly more dung around removed wallows.

I would interpret these results as a response to increased grass height. Short grass grazers in Hluhluwe moved away from removal areas presumably because grass growth after Rhino removals exceeded the off-take by grazers so that the grasses to grow out of the preferred height range of these species. The one result that doesn't fit into this scheme is the buffalo, which is a bulk grazer and should prefer large quantities of coarse grass. Hence Buffalo might be expected to show a different pattern, moving into Rhino removal areas with increased grass height and avoiding control areas. Instead Buffalo showed a pattern of decrease from controls to treatments in both Hluhluwe and Umfolozi. Buffaloes wallow extensively and it is possible that they visit the area around wallows largely in transit to the wallows themselves and that this is confounding the results of the dungcounts.

Grass composition

I did not find any indication of changes in grass species composition around the wallows. This indicates that the changes seen were purely structural and not a result of a change in the composition of the grass sward. This study was done over a period of 9 months perhaps too short a period to witness any species turnover. If there was a continued reduction in grazing pressure it may be possible that such a change would occur and that bunch grasses would begin to out compete and replace the lawn grasses.

General Discussion

I have demonstrated a change in grass height after White Rhino removals at the wetter end of the park as predicted by the hypothesis advanced in chapter 3. This change in grass height was difficult to detect within the heterogeneity present in the savanna and took the form of a reduction in the variance of grass height around removed wallows. However although this change in grass height is statistically significant was it necessarily biologically significant? Oneway to judge the

significance of the change in height might be to look at the reactions of other species of grazing animal. Judging by the response of impalas and other grazers, the change in grass height is indeed biologically significant. In Hluhluwe there were more short grass grazers in areas where White Rhino were present than in removal areas. In Umfolozi there were no significant effects of Rhino removal on other grazers. Thus Rhino removal has different effects at the two ends of the park, an example of the context dependent facilitation mentioned by Power *et al* (1996).

Another possible explanation for this result is that grazers are moving away from treatment wallows because the increase in grass height may increase the risk of predation by providing cover for predators. However I consider it unlikely that the small increase in grass height (<30cm) could have such an effect on the field of vision of impala, zebra and wildebeest.

Does this result indicate that the removal of White Rhino sets in motion a trophic cascade? If so is it a species level or community level cascade, as defined by Polis, (Polis et al. 2000). The changes after Rhino removals were evident after only one growing season but whether there is an effect beyond this time is unknown. Actual numbers of removed Rhinos were low, representing a small percentage of the population and it must be assumed that other individuals will eventually replace the removed Rhino through immigration. Changes in the numbers of other grazers was a result of a change in behaviour, not a change in the population of other grazers. Those grazers who prefer to feed on short grass areas moved away from the removed areas, presumably choosing to feed on short grass areas elsewhere. Would a sustained reduction in White Rhino density result not merely in changes in area utilised but also in declining populations of, for example, impala in Hluhluwe? This is plausible but I have no direct evidence of population changes as result of Rhino extirpation. If other grazer populations were significantly impacted by Rhino removal, this would qualify as a community level trophic cascade (Polis et al. 2000). If so it would have occurred in a complex terrestrial ecosystem which is unusual as most examples of population level trophic cascades come from either very simple (i.e. agricultural) or aquatic ecosystems. It has been suggested that complex terrestrial systems such as savannas are unlikely to show trophic cascades as they contain complex multilink food webs which have built in redundancies in the links between trophic levels (Strong 1992, Polis et al. 2000). However Owen Smith (1989) has argued that megaherbivores, such as the White Rhino, are keystone species whose extirpation can lead to complete

ecosystem shifts with cascading consequences. My results, for Hluhluwe, are consistent with his hypothesis. Unfortunately a rigorous test of the consequences of White Rhino extirpation requires an experimental manipulation beyond the scope of this study and I can only hint at the presence of such trophic relationships.

Arsenault and Owen Smith (2002) suggest that grazing facilitation may be a key factor during wetter parts of the year but that competition between grazers becomes more important during the dry months of the year when grass growth is reduced. It is this period that places a limit on animal populations. Grazing lawns become moribund over the dry season and during this period of the year short grass grazers shift their feeding patterns to longer grasses or browse (Owen-Smith 1988, Perrin and Bereton-Stiles 1999, Botha 2001). The result is that competition between species is reduced at this time of year when resources are at their most scarce. In light of this lawn grass areas would represent only a seasonal over abundance of food. Yet the increased food quality provided by grazing lawns must be beneficial to short grass grazers, even if only available in the summer. By choosing to graze on lawns grazers must be maximising some dietary quantity and increase their fitness. The physical condition of an animal at the onset of the dry season has been demonstrated to affect calving success in ungulate species (Arsenault and Owen-Smith 2002). Hence access to grazing lawns might therefore influence population numbers by effectively reducing the winter bottleneck in food supply by increasing summer nutrition.

Conclusions

I have demonstrated a context-dependent feeding facilitation by the White Rhino. During the wet season in Hluhluwe the removal of the White Rhino resulted in a species level trophic cascade. As such the White Rhino can thought of as a strong interactor (or depending on your definition, keystone species), in mesic savannas as it appears that other species of grazers cannot exert a controlling influence on grass height. Other species of short grass grazers moved out of areas from which White Rhino were removed. By contrast in arid savannas White Rhino removals resulted in a net influx of other grazers into removed areas and the other species of grazers were capable of controlling grass height.

The effects seen, although small and perhaps temporary, were the result of the removal of relatively small numbers of White Rhino from a high density

population. If the scale of the removals were larger it is very possible that the effect would be magnified, perhaps leading to a community level trophic cascade and population level facilitation.

This study took place over the wet season. It is possible that during the dry season as grass quality and abundance declines that White Rhino would move from facilitating other species of grazers to competing with them and that it is this period of the year that exerts a controlling influence on the populations of grazers ungulates.

6 Grazer induced shifts in fire behavior

Introduction

That both fire and grazing play important roles in shaping the structure of savanna ecosystems is widely accepted (Scholes and Walker 1993, Bond and van Wilgen 1996, van Wilgen et al. 2003). However these two important factors are usually studied separately and at a relatively small spatial scale. It is only recently that the interactive effects of fire and grazing on savannas have begun to be considered (Moe et al. 1990, Thompson-Hobbs et al. 1991, Van de Vijver 1999, Fuhlendorf and Engle 2001, 2004, Vermiere et al. 2004). Studies conducted as part of ZLGP within HiP have looked at grass grazer interactions within the spatial context of fires (Archibald et al. 2005) and they demonstrated that the nutritious regrowth of grass after burning has a magnet effect that attracts grazers away from heavily grazed patches including grazing lawns. This resulted in the recovery of grass height on grazed patches (Archibald and Bond 2004). The magnitude of this effect depended on the distance of the grazed patch from burnt areas and on the spatial scale of the burn itself. Grazed patches at a distance of more than 1.5km from a burn remained unaffected. Large frequent fires had a homogenising effect on the grass layer promoting tall bunch grass communities by not allowing grazing pressure to settle in any one area long enough for grazing lawns to develop.

Hence fire has been demonstrated to have an effect on the distribution of grazers and grass height within HiP. Fires require fuel in order to spread through the landscape and in grasslands and savannas this fuel is largely composed of grass. The amount of grass biomass (fuel) is correlated with rainfall over the previous 12 months (Balfour and Howison 2001, O'Connor et al. 2001). However clearly grazing also plays a major part in regulating the distribution of grass height, and hence biomass, throughout the system (chapter 3 and 5). If grass biomass is low as a result of heavy grazing then a heavily grazed patch effectively forms a firebreak and prevents fire moving through a system. For example fires cannot propagate across grazing lawns. Extensive work on fire behavior in Australia, (which has no large extant grazers), shows that burnt areas (or burn scars) from fires in stable weather conditions take the form of ellipses with the long axis corresponding to wind direction (Cheney and

Sullivan 1997, Catchpole 2002). Figure 6.0 shows a burn scar from HiP in an area of high grazing pressure and it can be seen that the shape of the burnt area is far removed from any idealized elliptical shape.

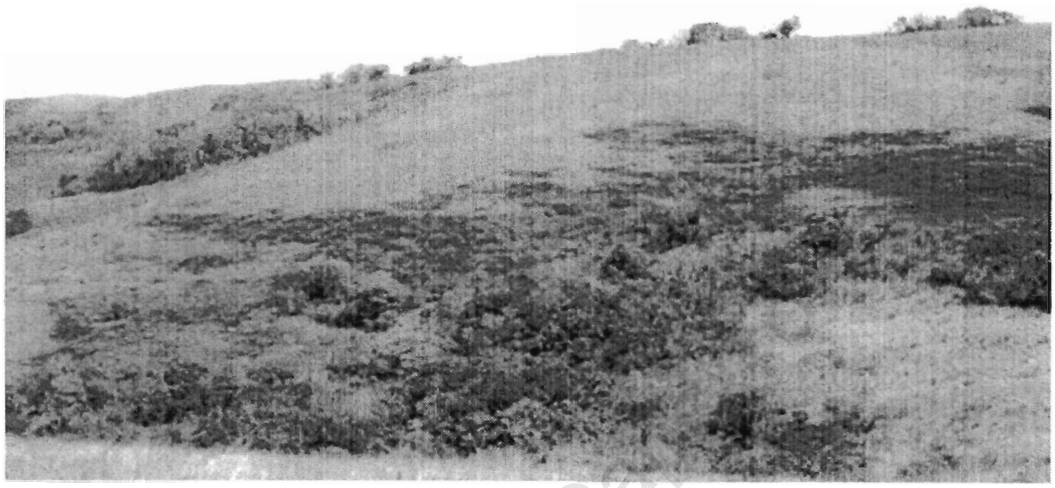


Figure 6.0. A photograph of a burnt area on Hlaza hill, Hluhluwe game reserve, October 2004. This hillside is frequently grazed by both White Rhino and herds of buffalo. Note that the edge of the burnt area is convoluted giving the burn scars a geometrically complex shape. It is far removed from an ellipsoid and suggests that grazing animals can affect the spread of fire through an area.

I have demonstrated in chapter 3 that grazing animals can alter the way fire moves through a grassland through their effect on grass height. In Hluhluwe this effect was largely due to White Rhino grazing whilst in Umfolozi other animals were also able to affect the spread of fire. However the response of fire to grazing was measured within our experimental exclosures at a scale of approximately 0.16 of a hectare and fires within HiP operate at a scale of hundreds or thousands of hectares (Balfour and Howison 2001). It is only if the effect of herbivores on fire remains at a larger scale that grazers could alter the ecology of the park through altering the fire regime.

My aim in this chapter is to investigate whether White Rhino can affect the distribution of fire within HiP at a landscape level through its demonstrated effects on grass height. If fire is able to effect the distribution of grazers within a system whilst grazers are also able to effect the distribution of fire there is the potential for a highly

dynamic system to develop with grazers and fire both competing for grass. Fire can be thought of as a non-specific herbivore and a system dominated by grazers or fire could occur (Bond 2005). My hypothesis would predict that due to increased grass biomass fires, and fire scars, would be larger and burn more completely in areas from which White Rhino have been removed (see figure 6.1). If other grazers were equally effective at reducing fuel loads there would be no difference in burn scar size and shape in removed and control areas. Furthermore results from chapters 3 and 4 suggest that this effect should be more pronounced in the higher rainfall end of the park (Hluhluwe) compared to the lower rainfall Umfolozi, where the effect of Rhino removal would be less pronounced or absent.

In this chapter I test this hypothesis by using satellite images to map burn scars in HiP and relating the size and shape of these burn scars to the maps of Rhino removals created in chapter 4.

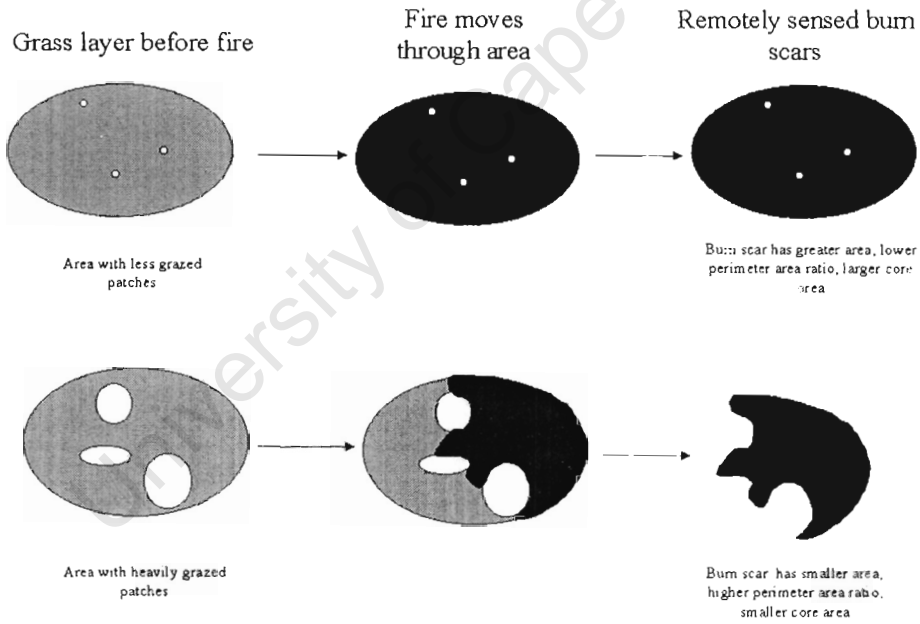


Figure 6.1. Proposed mechanism of how the effect of grazing can influence the size and shape of burnt areas

Methods

In chapter 3 the relationship described was between grass height and the probability of burning. I decided not to try and test this relationship directly at a landscape scale but to use the Rhino removals map developed in chapter 4 since Rhino grazing is an important determinant of grass height. I have already

demonstrated a relationship between grazing and grass height and between grass height and fire and so have a mechanism that could account for any differences in burn scar characters in control and removed treatments. A number of studies have used satellite data to try and quantify grass biomass (Henebry 1993, Goodin and Henebry 1997, 1998, Lobo et al. 1998, Archibald et al. 2005) although mapping of a continuous variable such as grass height presents difficulties compared to mapping fire scars. Since I am interested in the effects of Rhino grazing on the spread of fire, I studied variation in fire scars from satellite imagery in relation to the map of Rhino removals developed in Chapter 4.

In order to test the effect of Rhino effects on fire spread, I needed to map burnt areas at a scale large enough to observe landscape scale patterns in the whole of HiP, yet small enough to be observe the effects of grazing on the spread of fire. Remote sensing seemed ideal for this purpose particularly at the scale, resolution and price provided by orbiting earth observation satellites. There have been several methods employed to detect fires from space. Smoke produced as a result of the fire can be used to detect active fires (Kaufman and al 2003) or the heat energy produced by fire in the near infra red spectrum can be detected directly (Roy et al. 1999). These techniques are referred to as active fire detection and give good indications of spatio-temporal patterns of fire as they occur. Alternatively it is possible to detect the aftermath of fires, known as burn scars (or Fire Affected Areas by the Australians). Typically the darkened areas left after the passage of a fire is the result of carbonized materials and can last for some time. Sensing these areas has the advantage of detecting a 'memory' in the landscape that can show not just where a fire was at the moment that the image was acquired but in the entire period that it was alight. Hence mapping of burn scars is useful for quantifying burnt areas, and has been used in the calculation of fire return intervals (Hudak et al. 2004a).

Ash from grass fires with their fine fuels can be dispersed fairly rapidly by the wind. Regrowth of grasses and the resprouting of burnt trees can also be rapid particularly in tropical savannas. Hence the length of time that scars remains detectable by remote sensing is much shorter in savannas than in other biomes such as forests (Eastwood et al. 1998, Gerard et al. 2003). As burn scars get older they become harder to separate from the rest of the landscape. Fires in savannas can also be extremely patchy due to variations in the fuel load and this can lead to difficulties

obtaining a distinct spectral signature especially if burnt patches occur at a scale smaller than the resolution of the image. Methods do exist to examine variation that exists at a sub pixel size (Landmann 2003, Sa et al. 2003). These employ a technique called mixture analysis in order to estimate the proportion of a pixel composed of different landscape types but are complex to implement. (Pereira 2003) gives a good review of remote sensing of burned areas in tropical savannas.

Two approaches are commonly used to map burnt areas. The multi-temporal approach compares images of the same area taken before and after a fire and analyses for significant differences between the two. This is termed multi temporal change analysis (Roy et al. 2002). However this approach involves complications relating to detecting similar elements in the landscape under differing illumination conditions in the two images (Yuan and Elvidge 1996). It also requires the use of two images separated by a short time period which is not always feasible in the tropics and sub-tropics because of cloud cover obscuring the images. The second approach is called single post fire classification and involves only one image taken after the fire has occurred. This technique relies on recognizing the burnt areas within the image using the different spectral characteristics of reflected light in burnt and unburnt areas. Although multi temporal burn sensing has been shown to be more accurate, single post fire classification is preferable in terms of the cost of data and simplicity of processing (Koutsias and Karteris 2000).

A number of different orbiting platforms have been used for the remote sensing of burnt areas. These vary in the sensor resolution from coarse resolutions such as AVHRR with a 1 km pixel size, to instruments with 250m pixel size such as MODIS, to fine resolution instruments such as LANDSAT, SPOT and ASTER. There are also a number of newer systems in orbit, such as IKONOS, Quickbird and Hyperion that have pixel sizes in the range of 1-3m. However these images are expensive to acquire and have not yet been widely used. Justice *et al* (2003) give a surprisingly large list of 23 orbiting satellites that have been used for mapping fires. As a general rule sensors with coarse resolution generally have lower repeat times (i.e. MODIS instruments give updates of active fires four times daily, whereas LANDSAT only begins to repeat its coverage of the globe after a period of 18 days). The different sensors also vary in the number and width of bands that the electromagnetic spectrum is divided into (spectral resolution).

I used LANDSAT images to map burn scars because of their wide availability, relatively low cost, and suitable 30-meter pixel size. Although patches of lawn grasses do exist that are smaller than 30m, the datasets available at such a resolution were prohibitively expensive for this study. Some studies have used LANDSAT images as reference data in order to validate fire scar mapping by other platforms with coarser resolutions (Eva and Lambin 1998, Fuller and Fulk 2001). Only a few have actually utilised Landsat images to directly map scars (Russel-Smith et al. 1997, Koutsias and Karteris 2000, Bowman et al. 2003, Hudak and Brockett 2004b). Bowman reported visual and automatic interpretation of satellite images showing burnt areas of savanna was superior to semi-automatic and change analysis techniques in that they were able to detect burnt areas for longer. The advantage of visual interpretation is that it uses superior textural and pattern recognition abilities of human brains, which have yet to be incorporated into image classification packages.

I obtained Landsat 7 images from the Satellite Applications Center (SAC), at the CSIR in Pretoria and directly from NASA via the GLOVIS internet portal. Images were supplied processed to Level 1G meaning that they had been corrected for radiometric abnormalities and for the geometric curvature of the Earth. Images captured on the 15 September 2001 and on the 11th October 2002 were selected in order to map burn scars within HiP because of the minimal amount of cloud cover over the park in each scene and because they came from a time period late in the dry season corresponding to recent fires in the park. A third image was obtained for the 7th of November 2004, which, due to a satellite malfunction, was of reduced image quality[1]. This image was used to verify the accuracy of the burn scar classifications for the years 2001 and 2002 but was not used as part of the analysis of burn scars.

Image Classification

The images were imported into the program ERDAS Imagine (Leica Geosystems) and projected to a UTM zone 34 south grid. In order to produce a classification I needed to extract the spectral characteristics of burnt pixels. Burnt

[1] A malfunction onboard Landsat 7 occurred on May 31st in the Scan Line Corrector (SLC). The SLC is a pivoted mirror which compensates for the forward motion of the satellite during the time taken for the detector on the satellite to perform a complete scan of a single line of data. This mirror ceased to function on the 31st May 2003. After a period of investigation images became available again from September 2003 onwards. These images were captured in SLC-off mode. SLC-off mode images contain alternating lines of missing data that become reduced towards the center of the image giving the image a striped appearance. For further details see (Anon).

areas in the image could be readily identified when they were displayed using certain band combinations (e.g. Blue=band 5 Red= band 4 Green= band 3, see figure 6.2). I used the seed tool to extract spectral characteristics of the burnt areas, taking great care not to include areas that appeared at all ambiguous. Spectral signatures were extracted from each of the separate burns in the image as burn scars of different ages tend to have different spectral characteristics due to post fire re-growth of vegetation (Hudak and Brockett 2004b). The signatures were merged to form a single signature of burnt areas which was applied to the rest of the image using a parallelepiped classification scheme. The process of extracting a spectral signature and image classification was done separately for Hluhluwe and Umfolozi and the two images were then merged together to form a single image for the whole park. Separate spectral signatures were extracted from, and applied to, the images from 2001 and 2002. Finally a sieve filter was passed across the image to remove isolated pixels as was also done by Hudak *et al* (2004a). Overall this methodology largely follows that of (Hudak and Brockett 2004b) except that I did not initially transform the data using a principal component analysis.

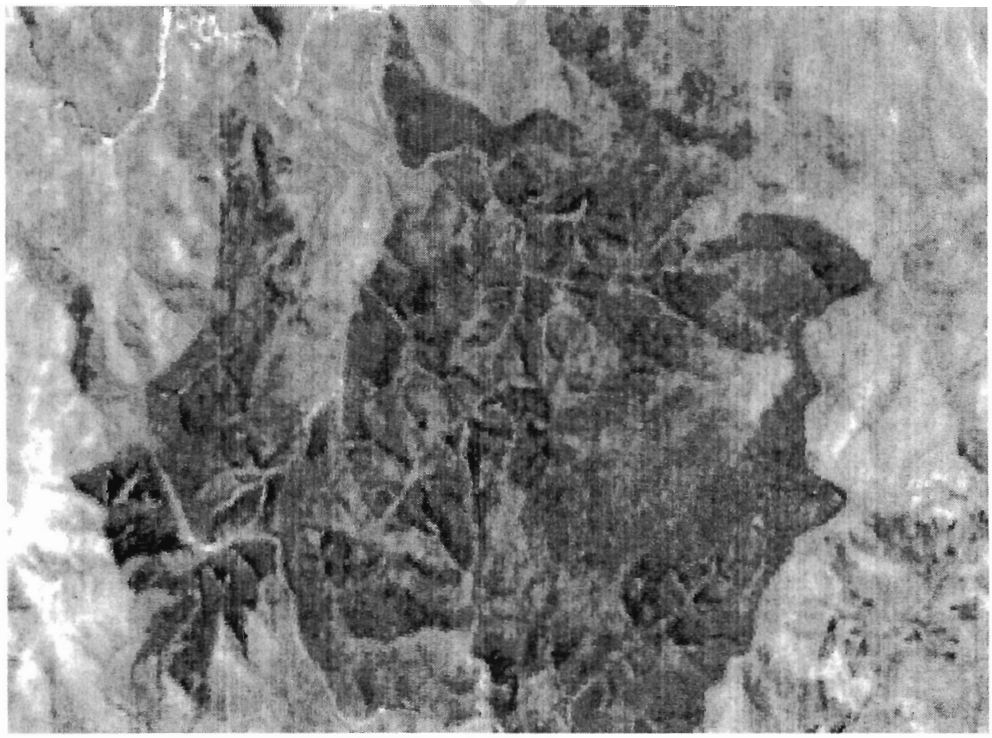


Figure 6.2.A scene from the central portion of Hluhluwe iMfolozi Game Reserve taken from a Landsat 7 image acquired on the 15th August 2002. This is a black and white reproduction of an originally colour image. Burnt areas can be clearly identified.

Image Accuracy Assessment

Before analysing the classified images of burn scars I tested the accuracy of the classification method. This was done by comparing the classified image to a reference image and then compiling an error matrix (Congalton 2001). The reference image is assumed to be accurate and can be derived from sources such as ground surveys and aerial photography. Classification errors can then be divided into two types of error: errors of omission and errors of commission. Errors of omission occur when the classified map fails to identify a burnt area correctly. Errors of commission occur when an unburnt area is incorrectly labeled as burnt in the classified image. I obtained reference data from two sources. During the 2004 fire season I recorded burnt areas on to a 1:50000 scale topographical map before digitizing them as polygons in an Arc View shapefile. This data was highly accurate but did not have good spatial coverage of the park. (To produce a hand drawn map of such accuracy for the whole park would have been extremely time consuming and would have defeated the object of trying to produce one through remote sensing). Hence this hand gathered data was suitable only for gauging the errors of commission. In order to measure the errors of omission I used fire maps produced by the section rangers. These were also digitised as ArcView shape files by KZN Wildlife staff at the Hluhluwe Research Centre. They had good spatial coverage but lacked accuracy as to the exact location of burn scar edges and pattern. The classified image should be more accurate than these maps for picking up the fine detail of burn pattern and hence these maps were useful only for measuring the errors of omission.

I used a Landsat 7 (SLC off mode) image from the 7th November to assess the accuracy of my classification method. The image was classified in the same as way that I had classified images from 2001 and 2002. I then randomly assigned 50 points to each class (burnt and unburnt) in both Hluhluwe and Umfolozi giving 200 control points in all. I did not use points that had been placed within the image gaps resulting from the SLC off mode of Landsat 7. Because the image was taken relatively late in the burning season some fire scars were up to 6 months old and because of post burn vegetation recovery they were difficult to detect. Hence I excluded burn scars that were greater than 4 months old from the accuracy assessment. The images of burn scars in 2001 and 2002 contained no burn scars of that age as they were taken earlier in the year (September/October). Control points were then compared to the reference

data in order to compile the error matrix, from which I calculated the errors of omission and its reciprocal, the producers accuracy, and errors of commission and its reciprocal, the users accuracy. Finally I calculated overall image accuracy and the KHAT statistic (Campbell 1996, Congalton 2001). KHAT statistics of over 80% are considered to indicate a good agreement between reference and classified data.

Image Analysis

Patch metrics are a series of indices designed to describe various aspects of the size, shape and distribution of patches within a landscape. They are often used (along with class and landscape metrics) within the field of landscape ecology to describe the distribution and patterning of patches, usually of habitat, within a landscape and how these change over time (Mladenoff et al. 1993, Leduc et al. 1994, Griffith et al. 2000). Metrics range from the fairly simple, such as the area and perimeter of a patch, to more complex measures such as the fractal index of a patch. Landscape ecology is still a relatively new science and the ecological implication of changes in these in these metrics, and what constitutes a significant difference between metrics, have yet to be clearly established (Turner et al. 2001). Another problem is that many of the metrics are not independent of each other but co-vary to a lesser or greater degree.

I calculated patch metrics of burn scars using the program FRAGSTATS version 3 (McGarigal et al. 2002). Fragstats has previously been used to characterise the shape of savanna fires (Hudak et al. 2004a) and for characterizing patches of different habitat in landscapes (Li et al. 2001). The burn scar classification was loaded into FRAGSTAT. Patches were then classified according to the 8-cell rule rather than the 4-cell rule, meaning that burnt pixels were grouped together in the same burnt patch when connected at the sides or at the corners rather than just at the sides. I chose this option as I believed it was a more accurate representation of the way fire moved through a landscape. FRAGSTATS outputs a text file giving patch metrics for each patch as identified by a unique number (patch ID). It also outputs an image file in which the pixels in each patch are given a value equal to the patch ID. Hence patch metrics can be referred to the patches from which they originated.

The output image containing these patch IDs was exported to ArcView 3.2 where it was overlaid with Rhino removal data extracted from the spatial database described in chapter 4. This data displayed the number and location of White Rhino

removed from the park in each calendar year in a 1 km by 1 km grid (figure 6.5). Where a burn patch was overlaid, either partially or totally, by a grid square from

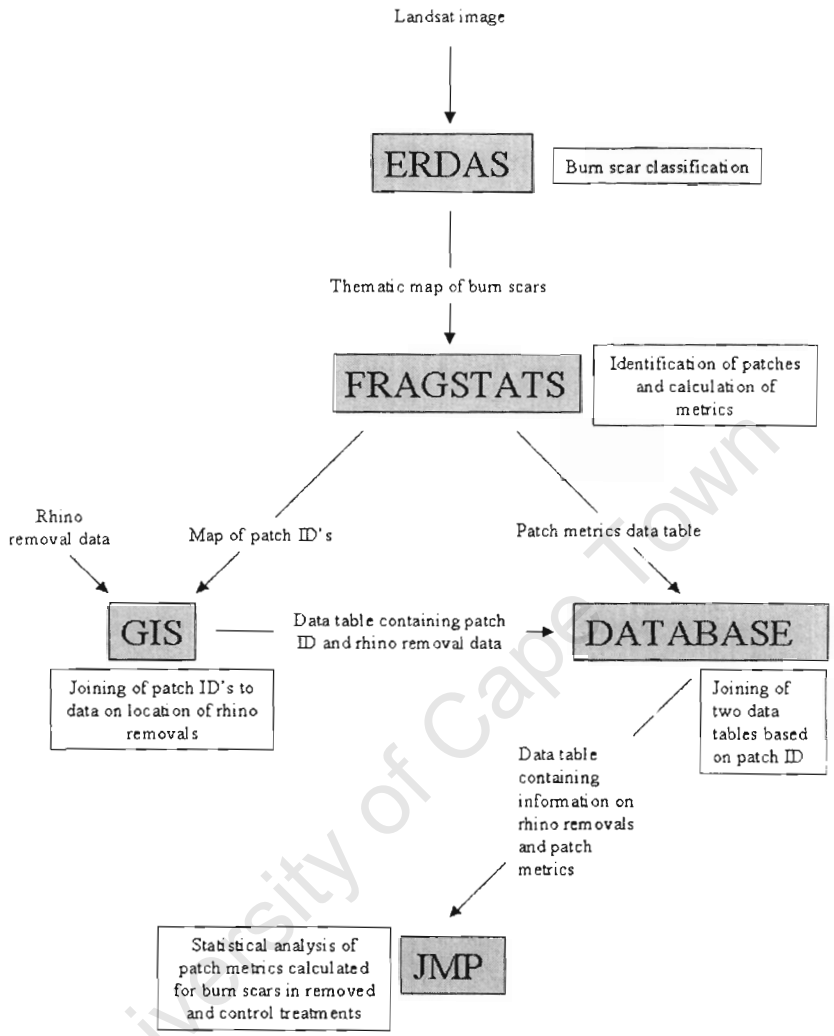


Figure 6.3. Diagrammatic representation of the process for calculating burn scar patch metrics and joining them to spatial data on White Rhino removals.

which White Rhino had been removed I assigned a value equivalent to the number of Rhino removed in that year to the attribute table of the burn scar. I used Rhino removal data for the 3 years previous to fires to join to the burn data. Most Rhino removals occur in the first half of the year (Mar-Jun) and most burns in the dry season towards the end of the year (Aug-Oct) meaning that a minimum of 6 months and a maximum of 3 years had elapsed between Rhino removals and the occurrence of fires. This was done for the both burn scar maps, 2001 and 2002.

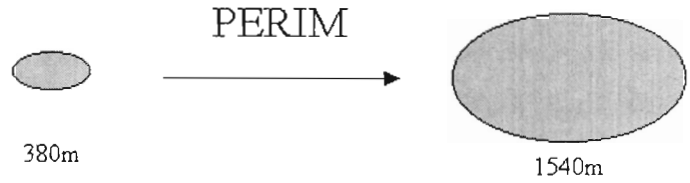
The attribute table of the burn scar image file containing both the Rhino removal data and the patch IDs were then exported and joined with the data table containing patch metrics using the patch ID as a unique identifier. The resulting table contained data about the size and shape of each burn scar patch identified in the image and also data pertaining to the number of White Rhino removed from the area around that patch. The data collation process is represented in figure 6.3.

I calculated the six patch metrics for each burn scar patch identified by FRAGSTATS within the landscape. These are described in detail in figure 6.4. Exact definitions and the formulations for all these of metrics can be found in the documentation accompanying the FRAGSTATS program (McGarigal et al. 2002).

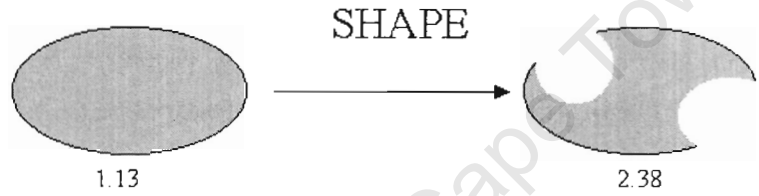
Statistical Analysis

The resulting data set was analysed in the statistical software package JMP 5.01. I assigned any burnt patch that had a Rhino removed from it in the three years previous to the fire as a 'removed' treatment patch. All other patches were designated as 'control' patches. I compared treatment and control groups by drawing box plots for each of the landscape metrics described above. Some of the metrics were displayed on a log scale in order to make any differences between groups clearer. I tested for significant differences between treatments using non-parametric statistics since the patch metric data was not

Area: The area occupied by a patch measured in hectares



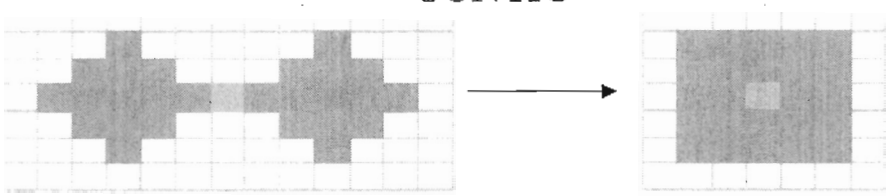
Perimeter: The length of the line surrounding a patch. Also includes the perimeter of any internal holes. Measured in meters.



Shape index: Calculated as patches perimeter divided by the perimter of a maximally compact shape of the same area. Value is 1 for a maximally compact shape and increases without limits for more complex shapes. Relates to the complexity of shape but does not vary with scale as PARA does

Figure 6.4 (continued on next page). Illustration of the various patch metrics used to describe the characteristics of burn scars and how they vary with shape. The metrics can be classified into three groups: basic metrics, metrics describing patch complexity and those describing its core area. The metrics AREA and PERIM fall into the first category. PARA, SHAPE and FRAC all describe the complexity of a shape (in other words how crenulated its outline is). A fire front which peters out due to lack of fuel biomass is likely to have a more complex outline and therefore higher values for shape complexity. Thirdly CORE, NCORE and CAI describe how much of a patch is close to an edge. It is highly affected by the presence of unburnt patches within a burn scar and should give an idea of how complete or patchy a burn was. High grass biomass should lead to less patchy burns and hence greater values for core area. Many of the metrics within these three groups measure similar shape properties in different ways and are not independent of each other but likely to co-vary. Numeric values are given to illustrate the effect of change in shape on the metric and the direction of change.

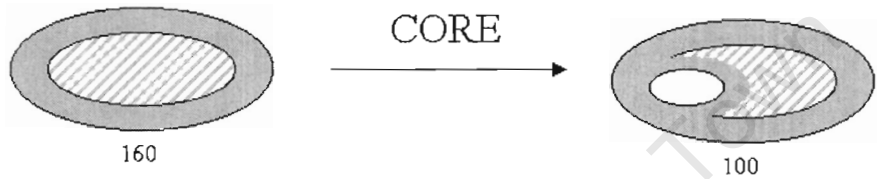
CONTIG



0.16 1.00

Contiguity: Is a measure of the isoloation of a pixel. Varies from 0 for a pixel completely isolated pixel from other like pixels to 1 for a pixel completely surrounded by other like pixels. Hence in the above example the lightly shaded pixel in the middle has a small values for contihuity on the right and amuch higher value on the left. Contiguity value for a patch is equal to the average value for all pixels in that patch. Another measure of shape complexity.

CORE



160 100

Core Area: The core area (hatched) occupies the area a set distance from the outside of a patch. I set this distance to 3 pixels or ~90m. Core area becomes reduced by internal patches of unburnt landscape hence giving an idea of how patchy a burn is. Measured in hectares

CAI

80% 60%

Core Area Index: The core are divided by the total area of the pacth.Units of measurement are percent and this metirc gives another measure of how patchy a burn scar is.

normally distributed (Mladenoff et al. 1993). The two tailed Wilcoxon test was used within JMP. The sample unit in this analysis is a 'burned patch' and these units are not uniform but can vary greatly in size. This provides a potential bias in my analysis since larger patches are able to exhibit more complexity than smaller ones. Large patches are also more likely to include Rhino removal squares and are therefore more likely to be classified as 'removed'. Hence removed patches are likely to reflect the characteristics of larger patches (i.e. large area and greater complexity) more than control patches. The heart of this problem is that burn scars can exist in the landscape at a scale an order of magnitude greater than the scale at which Rhino removals were mapped.

Figure 6.5. Map of burn scars (2002) and Rhino removals (previous three years) used to designate control and removal burns. Darker shades of removal squares indicate the number of Rhino removed. Burnt patches overlaid by removal squares were classified as removed and those not overlaid by removal squares were classified as controls. This illustrates the problem of scale mentioned in the text as points in burns classified as removed can be further away from removal squares when they occur in large burns than points in burns classified as controls.

In order to establish if any patterns observed were the result of genuine differences in fire behavior or merely an artifact of the scaling problem, I incrementally excluded the largest patches down to an area of 50 hectares (half the scale that Rhino removals were mapped at) and looked at the effect that this had on the differences in patch metrics between the control and removed groups. If

differences between control and removed groups were still evident when the larger patches were removed this would indicate genuine differences between the two treatments and not patterns produced as artifacts of scaling.

Results

Image Classification

The results of the image analysis of the satellite data are given in figure 6.7. These thematic images have two classes: Burnt and unburnt pixels.

Image Accuracy Assessment

The classified image from the 7th November 2004 that was used for the accuracy assessment is given in figure 6.6. Table 6.0 gives both the error matrix and the accuracy assessment comparing the classified image of burn scars from 2004 to the reference data.

Table 6.0 Results of the accuracy assessment performed on the classified image of burn scars from the 7th November 2004. a) error matrix; b) accuracy assessment.

a)

		Satellite image classfication		
		burnt	not burnt	total
Reference data	burnt	91	8	99
	not burnt	8	87	95
	total	99	95	194

b)

Producers Accuracy %	Errors of Omission %
91.9	8.1
Consumers Accuracy %	Errors of Comission %
91.9	8.1
khat	Overall Accuracy %
83.5	91.8

Image Analysis

A total of 155 burnt patches were identified in the 2001 image and 180 in the 2002 image by the FRAGSTATS image analysis program. However it should be noted that each of these patches did not represent an individual fire. Individual fires can be readily identified from the maps of burn scars (figure 6.7) as being groups of

burn scars separate from each other. The separate patches in a burn scar are the result of burnt patches being smaller than the resolution of the images. The area of these patches ranged from 0.1 to 3217 ha. In the three years before the two images were taken a total of 241 White Rhino were removed from 170 separate grid squares within the reserve. This led to 30 burnt patches being classified as removed in 2001 and 24 as being removed in 2002. All other burnt patches were classified as belonging to the control group.

Statistical Analysis

The distribution of the burn scar area was not normal but highly skewed with many small patches and only a few large ones. The box plots shown in figure 6.8 indicate the variation in and between burnt patches designated to control and removal groups for selected patch metrics. Table 6.1 gives the results of the two tailed Wilcoxon statistical tests done to examine the differences between the control and treatment groups. Results are presented in separate tables for the two ends of the park and are presented with data for the years 2001 and 2002 both separated and combined.

Secondly, table 6.2 presents the same data analysed so as to compare differences in patch metrics for the treatments at both ends of the park. Since there was little difference between data from 2001 and 2002 (table 6.1) data for the two years was combined in order to increase sample size.

The results of the analysis to test for scaling bias are given in table 6.3. The sample of burn scars was reduced by incrementally excluding the largest burn scar patches down to a burn scar patch area equivalent to half of the resolution of the scale at which Rhino removals were mapped.

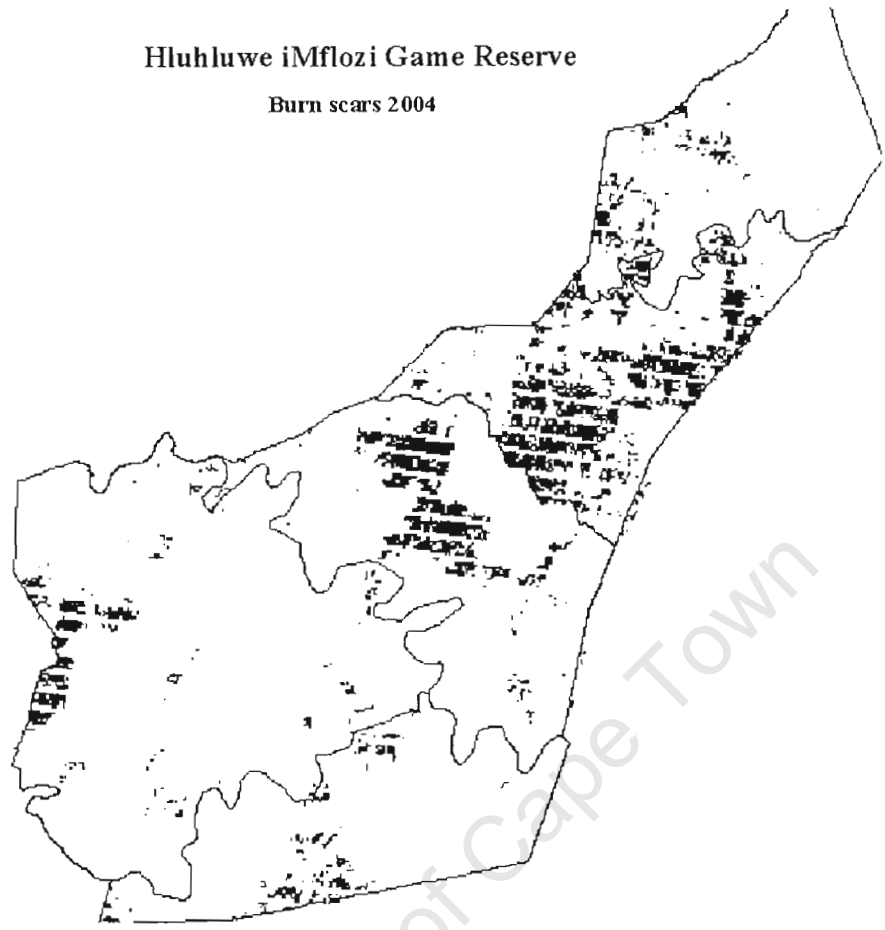


Figure 6.6. Classified Landsat 7 image from the 7th November 2004 showing burn scars. Note that this image was obtained in SLC off mode giving the image a striped appearance. Some burnt areas in the south of the park appear patchy due to the age of the burn scar.

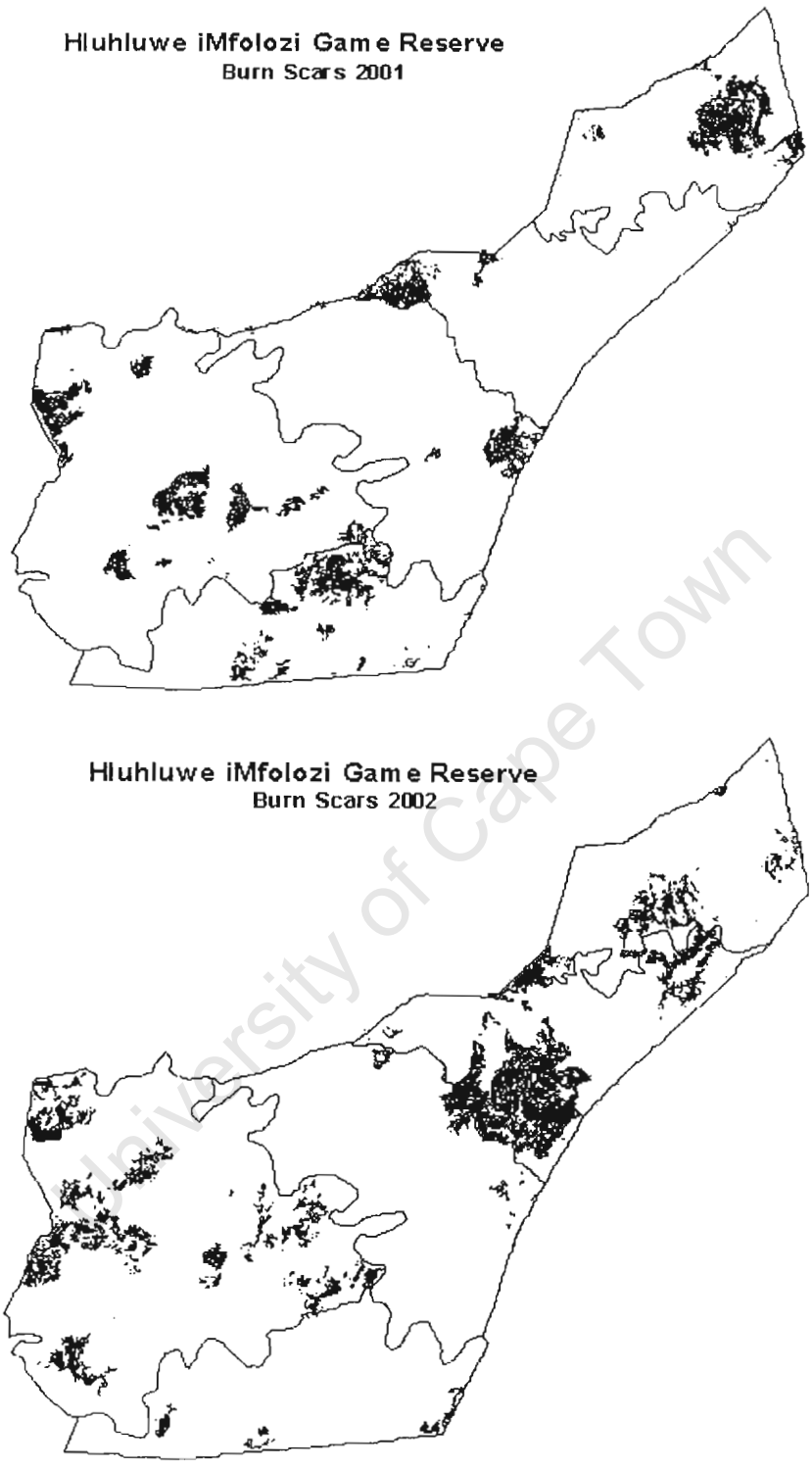


Figure 6.7.Burn scars in Hluhluwe iMfolozi game reserve as mapped from Landsat 7 satellite images. Acquisition dates are 11/10/2001 for the top image and 15/09/2002 for the bottom image. Image resolution is approximately 30m.

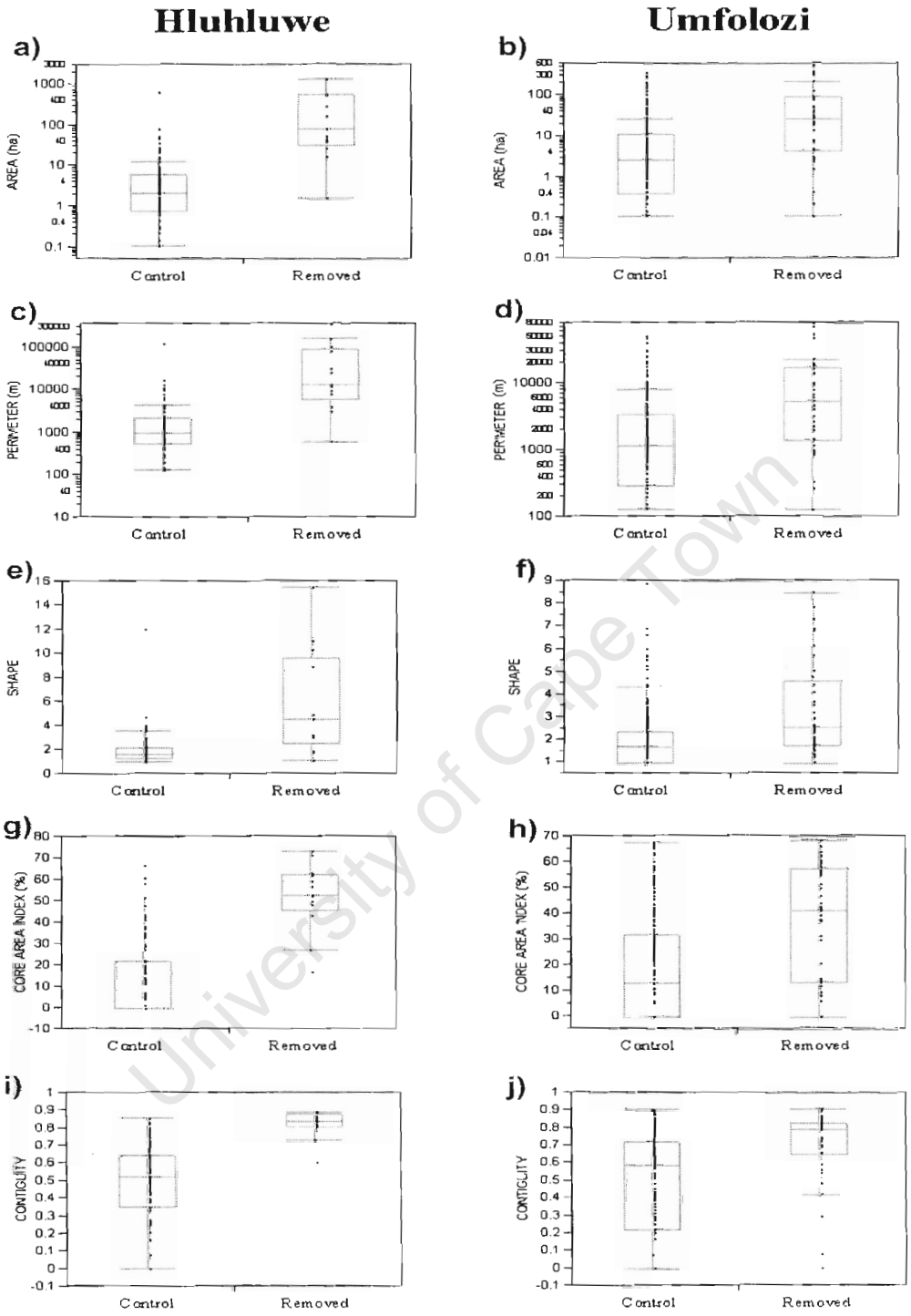


Figure 6.8. a) Area of burn scar in Hluhluwe in hectares from metric AREA, b) Area of burn scar in Umfolozi in hectares from metric AREA, c) Perimeter of burn scar in Hluhluwe in meters from metric PERIM, d) Perimeter of burn scar in Umfolozi in meters from metric PERIM, e) Burn scar SHAPE in Hluhluwe, no units f) Burn scar SHAPE in Umfolozi, no units g) Core Area Index of burn scars in Hluhluwe from metric CAI as a %, h) Core Area Index of burn scars in Umfolozi from metric CAI as a %, i) Contiguity vale of burn scars in Hluhluwe from metric CONTIG (no units), j) Contiguity values of burn scars in Umfolozi from metric CONTIG (no units). Data for 2001 and 2002 are combined. Note log scale on the y-axis of top two pairs of graphs.

Table 6.1

Comparison of selected burn scar metrics in removed and control areas in a) Hluhluwe b) Umfolozi. Results are given for both years in which burn scars were mapped and then as a combined value with data from both years grouped together. N=sample size. Mean and Median values are given for each group. Test statistics=Wilcoxon test. Patch metrics and units are described in the text.

Hluhluwe

Year	Treatment	N	AREA (ha)			PERIM (m)			SHAPE			CORE (ha)			CAI			CONTIG		
			Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z
	removed	6	362.62	121.75		52514	19239		6.27	4.95		196.56	61.75		10.74	4.96		0.84	0.86	
2001	control	46	3.47	1.47	<0.0001	1380	825	<0.0001	1.81	1.67	0.0001	0.55	0.00	<0.0001	518.54	6.10	<0.0001	0.43	0.47	0.0001
	removed	7	589.61	50.83		69030	9120		5.30	3.16		411.23	26.57		57.91	61.98		0.81	0.84	
2002	control	49	22.83	2.89	0.0042	5038	1216	0.0086	2.12	1.63	0.0035	10.96	0.58	0.0017	21.19	19.05	0.0003	0.53	0.58	0.0005
	removed	13	484.84	78.84		61407	13134		5.75	4.57		312.15	41.60		51.94	52.76		0.82	0.84	
combined	control	95	13.46	2.17	<0.0001	3267	988	<0.0001	1.97	1.67	<0.0001	5.92	0.00	<0.0001	12.88	0.00	<0.0001	0.48	0.52	<0.0001

Umfolozi

Year	Treatment	N	AREA (ha)			PERIM (m)			SHAPE			CORE (ha)			CAI			CONTIG		
			Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z
	removed	24	99.29	20.26		14066	4488		3.06	2.33		56.72	6.59		192.12	21.10		0.67	0.79	
2001	control	79	25.64	1.31	0.0008	4455	726	0.0015	2.03	1.60	0.0053	13.03	0.00	<0.0001	193.10	0.25	<0.0001	0.43	0.43	0.0002
	removed	17	98.16	53.72		16586	10184		3.81	3.00		57.70	22.96		43.47	55.61		0.73	0.81	
2002	control	107	22.00	4.48	0.0002	4441	1520	0.0001	2.16	1.81	0.0002	11.75	1.01	0.0003	23.63	22.86	0.0008	0.52	0.62	0.0005
	removed	41	98.82	27.55		15111	5412		3.37	2.56		57.13	13.43		36.63	41.50		0.70	0.80	
combined	control	186	23.55	2.74	<0.0001	4447	1164	<0.0001	2.10	1.71	<0.0001	12.29	0.43	<0.0001	18.52	13.06	<0.0001	0.48	0.59	<0.0001

Table 6.2

Comparison of patch metrics of burn scars of removed *versus* control areas between both ends of the park. Statistics are as described for table 4.1.

Park	Treatment	N	AREA (ha)			PERIM (m)			SHAPE			CORE (ha)			CAI			CONTIG		
			Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z	Mean	Median	prob>Z
hlu	removed	13	484.843	78.8436		61407	13134		5.7479	4.5667		312.2	15.38		51.937	52.762		0.4837	0.5217	
umf	removed	41	98.8231	27.5517	0.0328	15111	5412	0.0381	3.3716	2.5625	0.0521	57.13	5.073	0.0344	36.633	41.502	0.0371	0.4818	0.5875	0.0189
hlu	control	95	13.4563	2.166		3266.7	988		1.9735	1.6667		5.92	1.705		12.878	0		0.8233	0.8408	
umf	control	186	23.5477	2.7436	0.4316	4447.3	1164	0.5474	2.1035	1.7143	0.733	12.29	1.882	0.0345	18.516	13.064	0.0518	0.6976	0.7977	0.3697

Table 6.3

The results of incrementally excluding the largest burn scar patches from comparisons of treatment effects on the AREA patch metric. Prob>Z values are probabilities that the differences are due to chance calculated from a two tailed Wilcoxon test. Effect size is in hectares with positive values indicating that removed treatments were larger than control treatments. Both ends of the park are analysed separately with the two years grouped together. The original sample size (with both years grouped together) was 108 in Hluhluwe and 227 in Umfolozi.

burnt patches excluded (ha)		>3000	>1000	>500	>300	>200	>100	>50
prob>Z	hlu	<0.0001	<0.0001	<0.0001	<0.0001	0.0002	0.001	0.007
	umf	<0.0001	0.0001	<0.0001	0.0002	0.0003	0.0001	0.0081
effect size and direction	hlu	254	150	77	71	45	29	20
	umf	75	75	46	21	19	17	6
number of patches excluded	hlu	1	2	5	5	6	7	12
	umf	0	0	4	8	12	20	35

Discussion

This chapter has focused only on factors affecting the spread of fire through a landscape. However most of the biological effects of fire, such as its effect on trees and shrubs, are dependent on the frequency and intensity of fires (Higgins et al. 2000, Williams et al. 2002). I showed in chapter 3 that whilst fire spread was determined by fuel height, fire intensity was largely determined by weather variables at the time of the fire. However the effects of fire intensity can only occur if the fire can spread through the landscape.

When looking at the values calculated for the patch metrics it is wise to remember that these values are largely geometric quantities and not necessarily easily related to ecological phenomena. I hoped to gain the following ecological insights from the patch metrics. The area of a burn is a measure of whether a fire can spread through the landscape and is reflected in the metric AREA. Where a fire comes up against a matrix of short grass patches its progress through the landscape is likely to be slowed and its outline become more complex (see figure 6.1). As seen in chapter 3 if there are enough short grass patches, the progress of the fire can be stopped entirely. (Catchpole 2002) notes that 'length or edge indices may be useful for studies of post grazing fire effects'. Shape complexity is measured by the indices SHAPE, CONTIG and FRAC. Finally the patchiness of a burn can be thought of as the number of pixels within a burnt area that are not in proximity to a patch boundary. This is measured by the core metrics CORE and CAI.

The first thing to note about the data in figure 6.8 is that there is a lot of variation. This is particularly evident for the control grouping because it has a larger sample size than the Rhino removal treatment. The noise in the data is to be expected, as there are many other factors, such as fire weather and degree of fuel curing which are likely to affect the burns. Fuel load is also likely to be patchy even in the absence of herbivores, (chapter 5).

Despite these considerations, figure 6.8 shows that there are treatment effects in the metrics. All of the landscape metrics showed highly significant differences between the two treatment groups. These differences are consistent with our hypothesis of the importance of Rhino in maintaining grazing lawns which inhibit the spread of fires. For example, Rhino removal treatments contained larger median values of burnt patch size with larger core areas, i.e. cleaner burns with fewer unburnt patches.

Results were also consistent for both years in Hluhluwe and Umfolozi (Table 6.1) indicating that treatment differences were not biased by results from any one year. However there were indications that, in Hluhluwe, treatment differences were larger in 2001 than in 2002 perhaps because 2001 was a wetter year. Because there was little difference between the years I combined data from the two years in subsequent analyses in order to increase sample size.

Analysis of the exclosure experiments (Chapter 3) suggested a stronger response to Rhino removals in Hluhluwe. The patch metrics for burn area, shape and perimeter were not significantly different between control areas at either end of the park (Table 6.2) indicating that burns were of similar size and shapes in the two parks. However there was a significant difference in the metrics describing the core area (CORE and CAI) of control areas. Burn scars in Hluhluwe had a larger core area (area further than 3 pixels or about 90m from an edge of a burn) than scars in Umfolozi. This is likely to be because of lower grass biomass in Umfolozi resulting in patchier burns.

Burn scars in removed areas did show significant differences in Hluhluwe and Umfolozi for all the patch metrics analysed. Burn scars were significantly larger, more complex and less patchy in Hluhluwe than in Umfolozi. This is consistent with the hypothesis that White Rhino are important in maintaining short grass swards in Hluhluwe but less so in Umfolozi. In Umfolozi other animals were capable of controlling grass height in the absence of White Rhino (chapter 3). One would therefore predict that there would be no difference in burn scar size and shape between the removed and control patches in Umfolozi. The fact that there were significant difference between treatments in Umfolozi is somewhat surprising.

As noted in the methods, the sampling scheme was biased towards larger burnt patches being classified as Rhino removal areas. An alternative approach would have been to grid the whole park into 1 km squares (the same size as the resolution of Rhino removals) and compare patch metrics of burn scars within each grid square. Grid squares would be defined as either a removal or control treatment depending on whether White Rhino had been removed. However this approach is very laborious and poses several technical challenges, including the need to define edge of grid squares as either burnt or unburnt. Many of the metrics would be affected by artificial boundaries introduced by the grid size. Instead I tested for scaling artifacts by incrementally removing the large burns from the analysis. It can be seen from table

6.3 that removing the larger burnt patches had no effect on the significance or direction of the effect of Rhino removals on burnt patch area either in Hluhluwe or Umfolozi. Differences between burnt patches classified as either control or removed remained significant until patches of 50 ha were removed from the analysis. As this was half the resolution at which Rhino removals were mapped I conclude that the analysis was not biased.

Are there any other explanations that might account for the trends seen in the data? One possibility is that Rhino removal operations were restricted to open grassy areas that were more likely to burn. I tested this possibility by using a remotely sensed map of habitat types (Meyer 1998) and comparing the amounts of the different habitat types occurring in burnt patches designated as removed to the amounts of those habitats in the rest of the park. These values were plotted against each other and a straight line was fitted to the data. The R-squared value of this line was greater than 0.98 indicating that habitat types in Rhino removal areas occurred in the same proportion as in rest of the park, showing that differences in fire metrics between the treatments are not caused by differences in vegetation type removal areas.

The results of this study are consistent with the idea that White Rhino are creating firebreaks in the landscape by creating heavily grazed patches with such low fuel loads that they prevent fires from spreading. Thus fire is prevented from moving through the park and areas which may have sufficient fuel to burn are left unburnt. Unfortunately it was not possible to test whether the threshold relationship between the proportion of grass type present and area burnt detected in the ZLGP exclosures (Chapter 3) persists at the larger landscape scale. However the results of this landscape-scale analysis indicate that the inhibitory effect of Rhinos on fire spread is not affected by scaling up.

Little work has been done on the interactive effects of fire and grazing at larger scales other than the aforementioned studies conducted in HiP as part of the Zululand Grass Project. Wessman (1997) were able to distinguish between grazing and burning treatments using remote sensing in a tall grass prairie but did not examine the interaction between these two disturbance factors. Turner (1997) conducted some modeling exercises examining the effects of fire on winter forage availability for ungulates. Fuhlendorf and Engle (2001, 2004) and Vermiere et al. (2004) have studied the use of small patch burns for restoring the compositional and structural

heterogeneity of grasslands by producing temporary foci of grazing that produce a shifting mosaic of vegetation patterns across the landscape. This is interesting as it contrasts with the findings of Archibald and Bond (2004, 2005) in this park, who describe fire acting as a homogenizing agent by dispersing grazing pressure through the landscape. The important difference between the two studies is the scale of burns (about 4 hectares as opposed to hundreds of hectares).

From the data presented in this chapter it seems that the ability of the White Rhino to control grass height can affect the spread of fires within the reserve. Mean size of burnt patches were on average 25 times larger where Rhino had been removed. At what size would fires shift from creating heterogeneity to promoting homogeneity in the landscape? Would this size be affected by other variables such as numbers and species of other herbivores present? Could the removal of White Rhino lead to the homogenisation of the grass layer through promotion of larger burns? Within the park there has been a widely perceived shift from short grass communities to long grass communities (Bond et al. 2001) with a parallel increase of woody biomass in grasslands. I would interpret this as a shift from a mammal dominated system to a fire dominated system. Could it be that extensive historical removal of White Rhino and other grazers could have precipitated this shift? Unfortunately this is unlikely as the largest shifts in habitat are thought to have occurred in the northern end of the park, whilst Rhino removals have historically been concentrated in the south of the park.

7 Final Conclusions

The origins of open ecosystems, and the importance of large herbivores in maintaining them in the past, is still debated in places where these animals have gone extinct (Vera 2000, Svenning 2002, Mitchell 2005). The extinction of the Pleistocene global megafauna is hypothesized to have produced habitat changes that effected populations of smaller bodied grazers (Owen-Smith 1987, 1989, Zimov et al. 1995) and promoted fire (Flannery 1994). There are important implications for the management of natural areas if, indeed, an extinct megafauana created and maintained non-forested open ecosystems. For example, active human intervention and management could be seen as a necessary replacement for functions once served by the megafauna.

Areas in Africa which still retain an extant megafauna can throw some light upon these debates. Other species of African megaherbivore have been shown to have significant roles in structuring ecosystems and in facilitating other species (Verweij et al., Prins and van der Jeugd 1993, Fritz et al. 2002). In the United States Bison, though not strictly megaherbivores, have also been shown to have large ecosystem impacts (Knapp et al. 1999).

In this context, the ZLGP, to which this thesis contributes, set out to try and answer the following question: do White Rhino, due to their size, have a special controlling influence on the grass community types in HiP and what are the ecosystem consequences of this? Results of the exclosure experiments have shown that top down control of the grass layer is a reality in both the mesic and semi-arid rainfall ends of the reserve. At the mesic end of the park the influence of White Rhino was large, accounting for over 50% of the top down control (i.e. difference between grass height in the control and total exclosure) exerted by grazing mammals. In Umfolozi the effects of White Rhino grazing were much smaller and not so easily distinguished from that of other species of grazes, though it was still significant particularly at the larger landscape scales.

The 50% grass height increase seen when White Rhino were removed in Hluhluwe is particularly significant as it is in this height range that grass species which spread by stolons are replaced by species with an erect growth form. Structural

changes in the grass layer occurred rapidly in response to lowered grazing pressure, but we did not manage to detect any compositional change in the grass species even after 4 years of exclusion in the ZLGP plots. It appears that both lawn and bunch grasses can persist for some time in both community types. This suggests that changes between grassland states may be more complex than previously thought. The dynamics and life span of grazed patches and grazing lawns is perhaps an area in which further research may prove useful. We assume that lawns form as a result of a concentration of grazing but how, where and why this concentration develops is not understood. There is some limited evidence that they originate around nutrient hotspots such as termite mounds or old sites of human settlement (Feely 1978, Blackmore et al. 1990) (although the latter can only have become influential since the spread of man). Although a few lawns in HiP occupy large areas and have persisted through living memory, many others are small, just a meter or two in diameter and appear more transitory in nature (ZLGP unpublished data). The introduction of White Rhino into reserves in Africa previously unpopulated by megaherbivores could provide the opportunity to study some of these questions. If White Rhino are acting to facilitate other grazers it is reasonable to assume that their numbers might increase following introductions.

One obvious question raised by this thesis is why the smaller bodied herbivores are not able to replace the grazing effect of the White Rhino? Are they metabolically limited by their body size in some way? Possibly their reproductive rate posed a limited over the short time period of this study. There were simply not enough smaller grazers in the park to replace White Rhinos, but given enough time and continued removals, their populations could increase to a point where they were able to have an equivalent impact on the grass layer. Or perhaps their smaller body size places a control on the population by allowing predation to occur and this limits the population from growing.

The central focus of my thesis was to determine whether Rhino removal effects were detectable at larger spatial scales then those tested in the exclosure study. Using wallows as focal points, I was able to show that areas from which Rhinos had been removed within the previous year had significantly more taller grass particularly in the wetter end of the park.

Changes in grass height in the absence of Rhino grazing had two important consequences. Firstly in Hluhluwe there was a decrease in grazing pressure by other

short grass grazers in areas of Rhino removal in response to an increase in grass height. Hence White Rhino grazing does appear to effect the distribution of other grazers in the landscape, facilitating short grass grazers in mesic savannas, whilst appearing to compete with them in semi-arid savannas. Thus the 'keystone' role for the White Rhino in this savanna region is 'context-dependent' (Power et al. 1996). Whether these effects are enough to structure the populations of other herbivores in the park, rather than merely influence where they choose to graze, or whether these populations are limited by forage availability during the dry season is a complex problem that was not resolved in this study.

Secondly the removal of White Rhino altered the fire behavior in the park as short grass firebreaks in the landscape disappeared allowing larger fires to spread through the landscape. These fires were also less patchy than fires in control areas. Effects of Rhino removal on fire behavior were much stronger in Hluhluwe though also significant in Umfolozi. Over a number of years these grazer-induced changes in fire behavior would alter the fire regime by increasing the fire return interval, which could in turn have effects on the woody components of the system.

Grazing lawns are not only an important resource for grazing mammals. There is a growing literature about species of birds that require short grass areas (Wiens and Rotenberry 1981, Helzer and Jelinski 1999). Studies done as part of the ZLGP indicate that birds do not differentiate between lawn grass areas and other short grass areas such as recent burns or grazed bunch grasses. However grazing lawns are by far the most stable of these grass communities persisting in the environment and providing permanent patches of habitat (Krook 2005). Grasshoppers also have a different suite of species that exist on grazing lawns and there appear to be different tree species which recruit in grazing lawns as opposed to bunch grasslands (Bond et al. 2001). Hence grazing lawns contribute to the overall biodiversity of an area.

Large frequent fires have a homogenizing effect on the grass layer by dispersing grazing pressure across large areas of temporary regrowth, allowing heavily grazed patches to recover height. Frequently burnt areas had higher grass height (Archibald et al. 2005) increasing the likelihood of fires recurring. In a similar way grazing by the White Rhino increases the probability that an area will be regrazed both by it and other species of short grass grazer. (This is in contradiction to the line

of thought advanced from range management that grazing, in this case by domestic stock, promotes unpalatable traits within grasses (Tainton 1999)). Fire and grazers are therefore in competition for the same resource, each having the ability to capture the landscape into its own domain. At the mesic end of the park it appears that White Rhino are the only species which successfully 'competes' with fire. However fires can also increase grazing pressure, leading to areas of high grazer usage, if it they occur at a small enough scale (Fuhlendorf and Engle 2004). White Rhino grazing appears to limit the size of burns and may play a role in switching fire from acting as a disperser to a concentrator of grazing pressure. It would be useful to identify the point at which this occurs as it would represent the point at which a system would switch between the domains of consumer control – from fire to grazer. This could perhaps provide a fruitful future modeling exercise.

In high rainfall areas (mesic and above) a third vegetation type exists, in addition to the two states mentioned above, that of closed canopy forest (Bond 2005). The processes driving the transition from fire and mammal dominated systems to forest systems is as yet unclear. Dense bush appears to exclude fire allowing the establishment of fire sensitive forest precursor species. Grazing and 'overgrazing' in particular have been thought of as aiding woody encroachment by halting fires, hence allowing woody seedlings to establish and juveniles to prosper, resulting in dense stands of bush (Van Auken 2000, Langevelde et al. 2003). Yet grazing lawns are notable for their lack of woody saplings. Most encroachment in Hip occurs in bunch grasslands. This suggests that the heavy grazing that produces grazing lawns also *inhibits* woody plant recruitment. White Rhino may therefore play some role in effecting the transitions between grassland, dense bush and forest in mesic systems. This would be an extreme example of top down control.

Grazing lawns systems are absent from many other conservation areas in Southern Africa and it has been suggested that a lack of large grazers and rigid fire regime may have led to the loss of these grazing adapted systems (Bond and Archibald 2003). This would mean that HiP is very valuable as an intact fragment of ancient grazer/grass systems. HiP does manage to support an extremely high animal biomass/km^2, far in excess of that found in Kruger Park and comparable with that seen in the Serengeti ecosystem, all in a 90,000ha non-migratory fenced area. It is tempting to speculate about how this level of animal biomass is maintained in the

light of this thesis. Current conservation management places emphasis on creating or maintaining heterogeneity within a system. (heterogeneity being used as a synonymous with biodiversity). It is clear that, through its effects on the grass layer and on fire regime, the White Rhino can add significantly to the heterogeneity of the system and increase biodiversity by making available new ecological niches (i.e. grazing lawns). Whether there is enough evidence to qualify the White Rhino as a keystone species is unclear but it certainly plays an important role in the ecosystem.

With reference to the questions set out in the introduction of this thesis: Grazing lawns are biologically maintained by the 'top down' action of grazing animals. The White Rhino does play a greater role than other grazers in the top down control of lawns, at least in the mesic savanna. The removal of Rhino affects the distribution of other species that utilize grazing lawns in the system and also had an effect on the fire behavior through increased fuel load. This supports the theory put forward by Flannery (2002) that the extinction of the megaherbivores led to a change in fire regime.

It is now accepted that ecosystems are dynamic entities and that to effectively conserve biodiversity one must conserve the processes operating within them and this requires an understanding of how these processes operate. Correct management should take into account the evolutionary history of the area and be aware the management implications may be modified by factors such as rainfall (Mack and Thompson 1982, Fleischner 1994). By contributing to an understanding of these processes we hope to facilitate their management.

Appendix 1 Disc Pasture Meter calibration

During the Zululand Grass Project the height readings of the metal Disc Pasture Meter (DPM) have been extensively calibrated with actual grass height readings (n=1744). Annual and monthly grass clippings were taken from 1 square meter plots in order to measure grass productivity. Before plots were clipped a series of 5 DPM readings were taken. The grass was then labeled and placed in a paper bag to be dried in an oven at 90 ^{o}C for a minimum of 24 hours before being weighed to give dry grass height. These values of dry grass height (g/m^2) were plotted against mean DPM (cm) (from the 5 readings) and a linear regression line placed through the points.

Hence in order to convert the DPM height readings (cm) given in the text to actual height readings the following equation should be used:

$$\text{Total Height (g/m2)} = 12.62 + 26.11 * \text{DPM (height in cm)}$$
$$(R^2 = 0.73)$$

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